

**PROCESSES AFFECTING MACROFAUNAL COMMUNITY STRUCTURE IN  
SANDY SEDIMENTS ON THE NEW JERSEY INNER CONTINENTAL SHELF  
WITH A FOCUS ON THE DOMINANT POLYCHAETE, *POLYGORDIUS*  
*JOUINAE***

by

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## ABSTRACT OF THE DISSERTATION

PROCESSES AFFECTING MACROFAUNAL COMMUNITY STRUCTURE IN  
SANDY SEDIMENTS ON THE NEW JERSEY INNER CONTINENTAL SHELF  
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J. Fredrick Grassle and Judith P. Grassle

Continental shelves contain a rich array of habitats that appear significant for macrofauna and play an essential role in managing living resources. Yet, many habitats have not been adequately defined or quantified, temporally or spatially. Macrofaunal communities were examined at spatial and temporal scales within the context of known distributions of topographic habitats and associated sediment properties on the shelf off New Jersey, USA (39° 28' N, 74° 15' W). Focusing on a dominant polychaete, species identification and natural history information, together with manipulative experiments on behavior and habitat selection, provided a multi-pronged approach to research. Nested sampling designs were employed. Samples taken at large-spatial scales (m-km) showed that community differences were most pronounced among sampling dates, however, on any single date differences were related to crests and troughs in the rippled sandbeds. At small-scales (cm-m) community patterns and sediment properties corresponded with crests, flanks, and troughs. Concentrations of organic matter associated with finer sediments in troughs were ~1.2 times higher than in crests and flanks. Density of *P. jouinae* Ramey, Fiege and Leander, 2006, was higher in troughs than in crests. This species appears to thrive in sandy sediments from Massachusetts to southern New Jersey. The reproductive period occurred from May-August. Individuals that spawn, live for one

year. Recruitment begins no later than July. The smallest individual was 2.01 mm long providing an estimate of size at initial recruitment. It was hypothesized that heterogeneity in organic matter generated by rippled beds may influence small-scale distribution patterns of *P. jouinae*. In a racetrack flume under realistic flow, almost all *P. jouinae* moved through the sediment to patches containing higher amounts of organic matter in 48-h. Subsequent experiments showed that locating organic patches was not the consequence of a directed search. Rate of movement indicated that *P. jouinae* could potentially travel the wavelength of a typical ripple (14-30 cm) in 35-75 min. Thus subsurface movement is a plausible mechanism accounting for the similar small-scale spatial distributions of *P. jouinae* and food resources. This research reveals the fundamental influence of topographic differences in habitats on a member of the benthic macrofaunal community.

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## **CHAPTER 1:**

### **GENERAL INTRODUCTION TO DISSERTATION**

#### **SOFT-SEDIMENT COMMUNITY ECOLOGY: BACKGROUND TO THIS RESEARCH**

Like most areas of ecology, benthic ecology is concerned with describing spatial patterns of species distribution and abundance, and determining what factors or processes create the patterns observed at different scales (e.g., <1 m to 100 km). The role of habitat in influencing the structure and dynamics of populations and communities has been emphasized for both terrestrial and marine environments (e.g., Able et al. 2003; Diaz et al. 2003; Morris 2003; Zajac et al. 2003). Availability, quality, size, and spacing of habitat patches have direct effects on populations or communities by providing suitable habitat mosaics (often species specific) in some areas but not others (Chapman 1994; Underwood et al. 2000), or indirect effects by modifying interactions among individuals or species (Menge et al. 1985; Fairweather 1988). However, a top down approach where population and community patterns are studied within the context of defined habitats occurring at repeated intervals in space, has been more commonly employed in terrestrial and intertidal landscapes where habitats are readily visible (e.g., Underwood and Chapman 1996; Kent et al. 1997). Due to logistical constraints, research on subtidal infaunal or macrofaunal communities (infauna retained on a 300- $\mu$ m sieve) has more often focused on scale-dependent factors, without adequately defining or quantifying habitat(s) over time or space. This can confuse interpretation of patterns, especially if patterns are documented with samples collected at scales larger than those relative to

infauna. Moreover, spatial and temporal variability are generally interactive, so changes in one area may not occur in another, even when habitat patches are in close proximity (Thrush et al. 1994; Underwood 1996). Spatial-temporal interactions in the marine environment have been shown to affect local abundances of single species (e.g., Hogue 1982), interactions among species (e.g., Segerstråle 1962; Elmgren et al. 1986), and diversity of communities (Underwood and Chapman 1998). Much of this variability occurs because of individual and species differences in behavior, growth rates, and propagule dispersal, coupled with differences in dynamics among populations living in discrete habitat patches within a mosaic of different habitats (Underwood et al. 2000). At the same time, habitat selection by the organism also plays a central role in creating patterns and is an increasingly important theme in ecology (Morris 2003; Resetarits 2005).

It is well established that soft-sediment infauna are patchily distributed over many spatial scales (Volckaert 1987; Morrissey et al. 1992), and the ecological patterns and processes operating at one spatial scale may differ from those at another scale (Dayton and Oliver 1980; Levin and Huggett 1990; Whitlatch et al. 1998). It has been suggested that this patchiness (Whitlatch 1980), and the lack of appropriate spatial replication of samples (i.e. pseudoreplication) (Morrissey et al. 1992), have made it difficult to elucidate which factor (s) are most important in influencing infaunal patterns of distribution. In general, factors found to influence patterns over broad scales (10s to 1000s km) include water depth, circulation, and hydrodynamic processes (e.g., waves and currents) which are responsible for the distribution of surface sediments (Dyer 1986) and also influence food and larval supply. Salinity and temperature also create broad-scale patterns which

reflect physiological constraints on organisms. At relatively smaller scales (cm to km) infaunal distributions have most often been shown to be influenced by sediment properties, disturbance, predation, and competition (reviewed by Ólafsson et al. 1994; Snelgrove and Butman 1994; Bertness et al. 2001).

Nested sampling designs have been recommended for characterizing the large variation within marine soft-sediment communities, and to aid in understanding how community patterns are formed (Morrisey et al. 1992; Ramey and Snelgrove 2003). More recently, understanding the essential role of habitat in managing living resources such as fisheries has received renewed interest (Able et al. 2003; Diaz et al. 2003). Moreover, advances in imaging techniques have shown subtidal, soft-sediment landscapes to be heterogeneous and complex, containing a rich array of habitat structures (e.g., Able et al. 2003; Diaz et al. 2003; Zajac et al. 2003) that appear significant to bottom-dwelling organisms. For example, on the inner continental shelf off Maryland and New Jersey, significant relationships of juvenile fishes to topographic features at several scales indicate that seemingly small differences in physical habitat structure can make the difference between unacceptable and essential habitat, principally by providing refuges from predation (Diaz et al. 2003). Incidence (i.e. binary data [presence or absence] based on video images examined at 1-s intervals) of fishes was four times higher for areas with large ripples (>30 cm wavelength and ~10 cm crest height) relative to smaller ones (<30 cm wavelength and ~5 cm crest height). In another study, side-scan images of benthic landscapes in Long Island Sound identified six distinct large-scale (> km<sup>2</sup>) habitats defined by sediment grain size (Zajac et al. 2003). Within these, further habitat heterogeneity was present at spatial scales of square kilometers to meters, and even

smaller scales of  $<1\text{m}^2$  defined by distinct sediment patches, and biogenic structures (e.g., pits, mounds, and burrows) (Zajac et al. 2003). At scales ranging from square meters to kilometers, infaunal populations exhibited complex and spatially varying patterns of abundance in relation to habitat. Traditionally, infaunal studies have defined habitat based on broad-scale changes in sediment type, and distribution patterns have been related to differences in sediment properties, grain size being regarded as most important (Gray 1974, 1981; Etter and Grassle 1992). Far less is known about the causes of these observed patterns and about how sediment properties other than grain size and topographic features, within areas of “defined” sediment types, affect the typically high smaller-scale patchiness (Gallucci et al. 2005).

The morphology of ripples may be important in explaining the spatial distribution of benthic microalgae and meiofauna (infauna retained on a  $63\text{-}\mu\text{m}$  sieve) in sediments disturbed by waves (Kendrick et al. 1998), and heterogeneity created by ripples may be a source of microhabitat specialization and resource partitioning (Hogue and Miller 1981). For example, the interaction of near-bed flows with topographic features such as ripples and biogenic structures can enhance deposition of particulate organic material (POM) to the sea bed (Eckman 1990; Yager et al. 1993; Pilditch 1998). This is accomplished by creating regions of reduced shear stress, as well as through enhanced advective porewater exchange in sandy sediments driven by horizontal pressure gradients (Huettel et al. 1996). In oscillatory flows, ripples (0.7-cm height and 3-cm wavelength) were found to enhance porewater exchange rates by factors of 6-15 (Precht and Huettel 2003). In an attempt to mimic sediment and hydrodynamic conditions representative of continental shelf environments, Pilditch and Miller (2006) used an oscillatory water tunnel and



cultured diatoms as a tracer for particulate organic matter to show greater diatom deposition (3.5 x) and penetration depths (4-5 cm) in ripple troughs, compared with crests (<2 cm). This pattern, and total diatom flux, were consistent over a 3-fold variation in ripple wavelength (17-50 cm) and 4-fold variation in ripple height (1.4-7.7 cm) (Pilditch and Miller 2006). Photographs of a non-cohesive sandy rippled bed in the southern North Sea indicate that ripple troughs contained organic-rich material or “benthic fluff” which was clearly distinct from the sand bed. Its presence was greatest in May after the phytoplankton bloom but was still evident in January (Jago and Jones 1998). In both cases, higher concentrations in and on the sediment in ripple troughs might affect the abundance of certain deposit feeders.

Abundances of infauna inhabiting crests have been described as different from those in troughs (e.g., Sameoto 1969; Grant 1981) with some taxa having significantly higher abundances in troughs than in crests (Barros et al. 2004) and vice versa (Grant 1981). Organisms may be passively transported to (via bedload transport or resuspension or both), or actively select areas on ripples experiencing different flows (Eckman 1979). For example, small boundary shear-stresses may passively transport and deposit macrofauna to troughs of ripples (Eckman 1979), and reduced near bed-flow velocities in troughs may also allow larvae to swim and select habitat for settlement (Butman 1987). Flume experiments have shown that larvae are capable of habitat selection in realistic bottom flows (i.e., 5-10 cm s<sup>-1</sup>) (e.g., Butman et al. 1988). In general, larval dispersal and habitat selection are viewed as the primary factors responsible for observed population and community patterns (reviews by Scheltema 1986; Butman 1987; Underwood and Fairweather 1989). However, infaunal species with complex life histories have a number

of mechanisms for dispersal and selection of new and existing habitats. Post-larval (i.e., larvae that have completed metamorphosis and undertaken a benthic existence) dispersal, whether active or passive, has also been shown to influence the structure and dynamics of populations and communities (reviewed by Günther 1992; Armonies 1994). For example, transport of juvenile *Mya arenaria* in Barnstable Harbor redistributed individuals at scales of 10s to 100s of meters (Hunt and Mullineaux 2002), and flume experiments indicate that hydrodynamics and behavior played a role in the transport of juvenile bivalves, *Mya arenaria* and *Mercenaria mercenaria* (Hunt 2004). Furthermore, field and laboratory studies have shown that many bivalves drift using their byssal threads, and redistribution of juvenile *Macoma balthica* in the Wadden Sea leads to predictable, relatively large-scale seasonal shifts in the location of their populations (Beukema 1973; Beukema and Vlas 1989). Macrofauna may also move below the sediment surface, which is likely to be important in forming patterns at relatively smaller spatial scales, a topic that has been little studied since the experiments by Gray (e.g., Gray 1967; 1974).

Several studies in physically active intertidal and subtidal areas have suggested that active selection by post-larval stages is responsible for observed distribution patterns in rippled beds (e.g., Sameoto 1969; Grant 1981) but this hypothesis was not experimentally tested, and it is impossible to determine which mechanisms are at important, based on abundance patterns alone. If active selection is important, then patterns may be a result of macrofaunal responses to a variety of different food patches produced by small-scale variation in water flow (VanBlaricom 1982; Snelgrove and Butman 1994). For example, predatory amphipods have been observed to occur in higher abundances beneath ripple crests associated with meiofaunal prey, while ripple troughs

contained higher abundances of sand-browsing amphipods (Fenwick 1984), both predictable responses to food supply (Pilditch and Miller 2006). Because ripples migrate, it is likely that particulate organic matter (POM) also accumulates under ripple crests following sediment transport. Hogue and Miller (1981) showed that higher abundances of nematodes were found in crests at depths equal to the troughs. This pattern was believed to be a result of the nematodes initially being attracted to the organic matter accumulating in the trough and then becoming buried as the ripple migrated. Several experimental studies, unrelated to rippled beds, have also shown that juvenile and adult infaunal organisms actively respond to sediment food resources. Olivier et al. (1996) found that significantly more individuals of the subsurface deposit-feeding polychaete *Pectinaria koreni* left poor-quality sediment compared to high-quality sediment via water column movement. Similarly, there is evidence that depletion of resources triggers a swimming response by *Paranais litoralis*, an asexually reproducing marine oligochaete commonly found in ephemeral and disturbed habitats (Nilsson et al. 2000). Migrating worms were generally longer than non-migrating worms, indicating that migrating worms postpone reproduction (Nilsson et al. 2000). Once in the water column, worms apparently avoided re-settling where food resources were already exhausted. Stocks (2002) examined whether post-settlement water column movement is a passive process, or whether active behavior is involved, by conducting flume experiments with juvenile and adult polychaetes. Flow speed was at a velocity that did not cause sediment erosion but did cause bedload transport of anesthetized individuals. Polychaetes were placed in trays containing poor quality sediment, with the underlying assumption of the experiment was that as long as individuals were beneath the sediment surface at the start of the

experiments, then any movement must have involved, at a minimum, the individual exiting the sediment and moving to the sediment water interface (Stocks 2002). Two polychaetes, *Streblospio benedicti* and *Polydora cornuta*, displayed the most movement, whereas three other species displayed negligible movement. In any case, active habitat selection (whether for POM or some other sediment property) implies the capacity for horizontal and vertical movements of at least several centimeters (Eckman 1979), and species with highly motile larvae or post-larval stages are probably better suited for active selection than less motile taxa.

In summary, it is highly probable that community patterns result from a combination of passive deposition and habitat selection by larvae and post-larval stages. The relative importance of these processes is likely dependent on the heterogeneity of the environment, the spatial scale being studied, and the species in question. Thus, knowing what species are present and understanding their mobility, behavior, life history, and reproductive biology are critical to fully understanding the structure and dynamics of populations and communities. Unfortunately, the natural history of many infaunal species remains a “black box”, especially for polychaetes, which make up the largest portion of soft-sediment infaunal abundance. Of ~8347 described species of polychaetes (Hutchings et al. 2000) the complete life history is known for only ~3% (Giangrande 1997). Moreover, few sedimentary marine habitats have been well sampled and large numbers of previously undescribed species are all too common in benthic community studies (Grassle and Maciolek 1992; Snelgrove 1999).

## THE LONG-TERM ECOSYSTEM OBSERVATORY (LEO-15)

Continental shelf environments support a large number of commercially and recreationally valuable species. They are high energy, physically active areas with relatively permeable sandy sediments, and despite their importance, they have been little studied compared with other coastal environments. Research for this dissertation was conducted on the inner continental shelf at the Rutgers University Long-term Ecosystem Observatory at 15 m depth (LEO-15), located ~9 km off southern New Jersey (Fig. 1) (Von Alt and Grassle 1992). LEO-15 is ~3 km<sup>2</sup> in area and is dominated by Beach Haven Ridge (39° 28' N, 74° 15' W), a shore oblique sand ridge characteristic of 71 such ridges found off the New Jersey coast (McBride and Moslow 1991). Beach Haven Ridge is ~5 km long by 1.5 km wide with a maximum relief of 8 m between the ridge crest and trough on the shoreward side, with water depths of 6-16 m. Surficial sediments are mostly made up of medium and coarse sand (>250 µm), but zones of finer sediments (grain sizes finer than 250 µm) are present on both the landward and seaward sides of the ridge (Craghan 1995). The fine grained zone on the landward side is indicative of the exposure of lagoonal muds as the sandy sediment supply that overlies it is transported ridgeward. The fine grained area on the seaward side may be due to deposition of finer grained sediments transported seaward over the ridge crest (Craghan 1995). The Beach Haven Ridge area is also one of New Jersey's recurrent coastal upwelling centers (Glenn et al. 2004) characterized by episodic summer upwelling and downwelling events. It is influenced by hydrodynamic processes such as tides, waves, storms, and wind-generated bottom currents. Boundary layer studies have documented seasonal variation in bottom flow and the significance of energetic wave events for initiating and maintaining

sediment transport (Styles 1998). During a particularly active period when six tropical storms, some of hurricane strength, passed just east of LEO-15, Traykovski et al. (1999) found that mean alongshore currents on the southern landward side of the ridge (near Sta. 9, Fig.1.), measured 44 cm above the bottom, were 5 to 20 cm s<sup>-1</sup> and that cross-shore currents associated with the tides were generally  $\leq 8$  cm s<sup>-1</sup>. The critical erosion velocity of the sediment was 25 cm s<sup>-1</sup>. Moreover, Beach Haven Ridge is a mobile feature that is apparently moving offshore (Craghan 1995). This high level of physical activity profoundly influences the physical landscape and benthic communities living there.

Sediments and habitats in the vicinity of LEO-15 are complex and heterogeneous, consisting of a variety of bedforms, substrates, and biogenic structures (Able et al. 2003). Detailed characterization of substrates and habitats in the vicinity of Beach Haven Ridge was partially stimulated by renewed interest in understanding the essential role habitat plays in managing commercially and recreationally important species of fish (e.g., Able et al. 2003; Diaz et al. 2003). In situ observations of sediments and habitats in 1990-1994 using a variety of platforms (i.e., SCUBA diver hand held video cameras, remotely controlled vehicles, and a submersible) showed that sandy rippled beds were the predominant topographic feature, with ripple heights and wavelengths varying over time and space (Able et al. 2003). Ripple troughs were intermittently covered by varying amounts of shell hash, whereas other areas were flat or had gravel or clay sediments. Biogenic substrates consisted of patches and mats of tubiculous polychaete worms (e.g., *Diopatra cuprea*) and amphipods (Able et al. 2003). Over a six-week period from August to September 1995, ripple characteristics were measured in well-sorted sediments composed of coarse sand on the southern end of Beach Haven Ridge near Sta. 9 (Fig. 1)

(Traykovski et al. 1999). Ripple height varied from 3 to 15 cm and wavelengths from 10 to 100 cm. Ripples also migrated  $\sim 24 \text{ cm d}^{-1}$  with a maximum rate of  $80 \text{ cm d}^{-1}$ , when wave energy was greatest (Traykovski et al. 1999). Ripple migration was generally directed shoreward and ripples were symmetrical in shape which is the characteristic morphology created by wave-driven oscillatory flow.

Several research stations have been set up at LEO-15 to examine the consequences of upwelling and downwelling events, the different hydrodynamic regimes, and sedimentary habitats (Fig. 1). In terms of macrofaunal studies, research has focused on the economically important surfclam, *Spisula solidissima*, spanning topics such as larval supply during upwelling and downwelling (Ma and Grassle 2004, Ma 2005, Ma et al. 2006), larval settlement (Snelgrove et al. 1999, 2001, Weissberger and Grassle 2003, Ma 2005), early recruitment and predation (Garlo 1980; Weissberger and Grassle 2003; Quijon et al. 2007; Newby 2006), and behavior of this surfclam in a migrating rippled bed (Newby 2006). Research for this dissertation addressed whether macrofaunal community patterns at multiple spatial (i.e., m to km) and temporal scales (i.e., months) can be related to topography. More specifically, this research defined and characterized soft-sediment benthic habitats and their associated macrofaunal communities at relatively small scales (i.e., cm to m), and investigated what features of these habitats (e.g., sediment properties) may be important in influencing the macrofaunal patterns observed. A new species of a highly abundant and often dominant polychaete, *Polygordius* sp. A. at LEO-15 was described, and the reproductive biology, circulatory system, habitat preferences, and ecological importance of this species were also investigated.

Prior community level studies have examined macrofaunal patterns in relation to broad-scale sedimentary habitats based on sediment type over relatively large spatial scales (km). Snelgrove et al. (2001) found different macrofaunal communities at two stations with contrasting sediment grain size a few kilometers apart. *Spisula solidissima*, the polychaetes, *Polygordius* sp. A (now *Polygordius jouinae* Ramey et al. 2006) and *D. cuprea* were important components of the community in coarse sandy sediments (Sta. 9: ~500- $\mu$ m, Craghan 1995) located on the southern landward side of Beach Haven Ridge (39° 27.69' N, 74° 15.81' W; ~12-m depth) (Fig. 1). Recent recruits of *S. solidissima* can be very abundant with densities as high as  $2.4 \times 10^5$  individuals  $m^{-2}$  (Weissberger and Grassle 2003). At times, *P. jouinae* has made up >50% of macrofaunal abundance with densities as high as 98,400 individuals  $m^{-2}$  (Snelgrove et al. 2001). In muddy-sand (St. 32: ~74  $\mu$ m, Craghan 1995) on the northern, landward side of the ridge (39° 29.29' N, 74° 14.48' W; 16-m depth) the bivalve *Nucula annulata*, the polychaete *Mediomastus ambiseta*, and oligochaetes were the dominant macrofauna. The relatively large tube building polychaete, *Diopatra cuprea*, was also common at this station. These results are consistent with previous studies from this area (Garlo 1980) and more extensive studies on the Mid-Atlantic Bight continental shelf (e.g., Boesch 1979) that revealed similar sedimentary associations. Diversity ( $H'$ ) was significantly less in individual cores collected from the coarse sand sediments than in muddy-sand (Snelgrove et al. 2001). In terms of epifaunal organisms, the sand dollar *Echinarachius parma* and the burrowing anemone *Ceriantheopsis americanus* are commonly present at a sandy offshore station (Sta. 30: ~500  $\mu$ m, Craghan 1995) (Sta. 30: 39° 28.8' N, 74° 13.29' W; 16-m depth) (Grassle et al. 1999).



At large distances and spatial scales (km), such as those described above, the dispersal and habitat selection that form the template for community patterns are considered to operate primarily during the planktonic larval stages for most macrofauna (e.g., Scheltema 1986). At LEO-15, Ma (2005) examined the relationship between larval surfclam concentrations and settlement at Sta. 9, Sta. C (39 27.85 N, 74 15.11 W; ~ 12-m depth), and C2 (39 23.24'N, 74 12.75 W; 20-m depth) (Fig. 1). Automated, Serial Zooplankton Pumps (designed by Doherty and Butman 1990) moored 1 m above the bottom measured larval surfclam concentrations every 4 h, and azoic sediment trays left in situ for 3-4 d (for three out of four deployments) were used to measure larval settlement. Spatial and temporal variation in larval supply was controlled by upwelling and downwelling circulation, and surfclam settlement was influenced by larval supply (Ma 2005). In a different study Snelgrove et al. (1999) examined whether larval selectivity at settlement contributes to distributional patterns of macrofauna through three 3-5 day reciprocal sediment transplant experiments at the coarse sand Sta. 9, and muddy-sand Sta. 32. It was demonstrated that habitat selection by settling larvae of some macrofauna may set initial distribution patterns, and differences in larval supply, which vary spatially (km) and temporally (weeks) can affect settlement intensity. Specifically, larvae of *S. solidissima* selected coarse sand over muddy-sand, and capitellid polychaetes selected muddy-sand over coarse sand, regardless of site. Larvae of both taxa selected sediments typical of adult habitats, displaying selectivity consistent with previous flume experiments (Grassle and Butman 1989; Butman and Grassle 1992; Snelgrove et al. 1998). In addition, plankton pump samples taken at the stations during the experiments suggested that significant differences in supply of surfclam larvae contributed to

between-station differences in settlement over the 3-km scale (Snelgrove et al. 1999). Although several other taxa at LEO-15 also exhibited selectivity consistent with field distributions (e.g., *P. jouinae*), others were non-selective, and in both cases it was unknown whether individuals were of recent settlement size. However, Snelgrove et al. (1999) found that surfclams in some of the settlement trays were larger than expected for recent recruits and determined that these individuals were earlier recruits that had moved into the trays through post-settlement transport and selection. Several authors have noted that species living in disturbed or physically active habitats tend to disperse more than species living in stable habitats (e.g., Palmer et al 1996). Thus, post-settlement movement, whether passive or active, may be an important mechanism influencing macrofaunal community patterns over relatively small spatial scales at LEO-15.

Besides larger scale community differences among stations, macrofaunal communities within stations at LEO-15 are highly patchy (Grassle et. al. 1999), and in order to provide sufficient within station characterization to resolve the larger scale patterns among stations, researchers have employed a nested design. For example, within each station (each station: 200-m diameter), three 60-m diameter areas called “substations” were set up and within each of these a pair of macrofaunal samples including one from a crest and the other from a trough, were collected at three points. Yet, whether spatial scale is more or less important than habitat type in capturing community variation within stations remains unresolved. Moreover, examination of spatial patterns alone (not within the context of habitat type) does not provide a comprehensible ecological framework for examining the mechanisms that are important in creating smaller scale patterns, which was the topic of interest in the present study.

Using the same nested sampling design described above, Snelgrove et al. (2001) noted that whether macrofauna came from crests or troughs of ripples had no bearing on the observed differences in community structure between two stations located ~ 4 km apart (Sta. 9 vs 32). These communities, however, were very distinct in terms of sediment grain size (sandy vs. muddy-sand), which may have been more important than topography in influencing community patterns at this relatively large spatial scale. Another study at LEO-15 provides some evidence that species groups respond to changing patterns in topography such as sand ripples (Grassle et al. 1999). I examined whether crests and troughs of sand ripples support different macrofauna within and between two stations located ~ 4 km apart (Sta. 9 and Sta. 30), with relatively homogeneous sandy sediments. This study also examined whether infaunal communities differ among defined habitats such as ripple crests, ripple troughs with shell hash, troughs without shell hash, and ripple flanks at a single station and date.

Macrofaunal larvae and post-larval stages may be passively transported to or actively select areas on ripples experiencing different flows (Eckman 1979). Previous macrofaunal sampling in sandy rippled beds at LEO-15 revealed some species-specific patterns of abundance related to either crests or troughs. For example, Newby (2006) noted higher abundances of *S. solidissima* in either crests or troughs, depending on location and date. In an effort to understand these inconsistent distribution patterns, flume experiments were conducted to investigate the movement of juvenile *S. solidissima* in a migrating rippled bed. Most clams did not move with the ripples but some were eroded out of a ripple crest and carried a short distance downstream, where they were deposited in a trough and re-burrowed (generally the downstream trough adjacent to the crest)

(Newby 2006). Moreover, the deposit-feeding polychaete *P. jouinae* is commonly found in higher and more variable densities in ripple troughs than in crests (Grassle et al., unpubl. 1999). Several studies in physically active intertidal and subtidal areas have suggested that active selection by post-larval stages is responsible for observed distribution patterns on rippled beds (e.g., Sameoto 1969; Grant 1981). Patchiness of resources, coupled with the behavior of species can determine the arrangement of individuals within communities (Thrush et al. 1989). Patches of fine organic flocs observed by divers on the surface of ripple troughs at LEO-15 (Petrecca, pers. comm.) could influence macrofaunal distribution patterns. The present research examined the importance of subsurface migration and active selection for food resources in creating small-scale patterns at LEO-15. Flume experiments were conducted to test whether the higher abundance of *P. jouinae* in ripple troughs than in crests could be causally related to active selection by this deposit-feeding polychaete for elevated levels of sedimentary organic matter derived from the organic-rich flocs typically associated with troughs.

## SUMMARY AND OUTLINE OF DISSERTATION

The present research was conducted at the Rutgers University Long-term Ecosystem Observatory at 15 m depth (LEO-15) off New Jersey where stations were set up to take advantage of the different hydrodynamic regimes and habitats present on the continental shelf. This study took an alternative approach to nested designs, which use blind or remote, random sampling methods. The focus was on the structure and dynamics of infaunal populations and communities at multiple spatial scales, within the context of known distributions of habitat types in order to detect variability in an ecological context

(e.g., Sisson et al. 2002; Zajac et al. 2003; Barros et al. 2004; Baptist et al. 2006). A key question was whether community patterns at a variety of spatial (i.e., cm to km) and temporal scales (i.e., months) can be related to defined topographic features, and what features of these habitats (e.g., sediment properties) may be important in influencing observed infaunal patterns. Both field observations and manipulative experiments were conducted, emphasizing species behavior, habitat selection, and natural history information for a dominant, previously undescribed polychaete *P. jouinae* Ramey, Fiege and Leander, 2006, providing much needed background on species distributions in an environmental context (Tanaka 2003; Morris 2003; Resetarits 2005; Hewitt et al. 2007). More specifically, this research aimed at bridging the dichotomy between correlative and manipulative studies by nesting manipulative studies within a correlative framework, as recommended by Hewitt et al. (2007). Based on correlative field data, flume experiments were designed to examine processes that may be responsible for the small-scale distribution patterns observed for *P. jouinae*.

Chapter 2 is entitled, “Do ripple crests and troughs support different macrofaunal communities?” (Ramey, unpublished). The primary goal was to examine whether species inhabiting ripple crests and troughs in sandy sediments differ, and to determine whether observed macrofaunal patterns change spatially (i.e., m to km) and temporally (i.e., months). Paired crest and trough samples were collected in several different months, from two stations ~4 km apart, where sediment grain size was relatively similar. Community differences were most pronounced among sampling dates, however, when only a single date was considered, differences were related to crests and troughs. In July and October, further variation, beyond that of habitat, was attributed to the largest spatial scale (4 km)

between stations. Differences in the relative abundance of dominant taxa including *P. jouinae*, *S. solidissima*, and Nemertea spp. were important in driving observed community patterns. Most notably, density of *P. jouinae* was consistently higher in troughs than in crests at both stations.

Chapter 3 is entitled, “Ecological heterogeneity: small-scale, patchy distributions of macrofaunal species in an ecological context” (Ramey, unpublished). This research set out to define and characterize soft-sediment benthic habitats and their associated communities at relatively small scales (i.e., cm to m). It also investigated some of the features of these habitats (i.e., sediment properties) that may influence observed macrofaunal patterns. Habitats were characterized at a single station, using camera and video images, in conjunction with sediment analyses to measure grain size and food quality measures (e.g., chl *a*, phaeophytin, carbon, and nitrogen). Macrofaunal cores were taken from each of four habitats, namely ripple crests, ripple flanks, ripple troughs with shell hash, and troughs without shell hash. Community patterns and sediment properties were related to three topographic habitats (i.e., crests, flanks, and troughs (+SH [shell hash] and –SH), frequently encountered within areas  $< 1 \text{ m}^2$ . Thus, communities and sediment properties within an area  $< 1 \text{ m}^2$  were more different from each other than from replicate samples taken further apart (2 to 44 m). Differences in the relative abundance of dominant taxa including *S. solidissima*, *Tellina agilis* and Nemertea spp. Concentrations of particulate organic carbon, associated with finer sediments in troughs (SH and –SH), were ~1.2 times higher than in crests and flanks, and chl *a* and phaeophytin contributed to considerable within habitat variability. Total macrofaunal density and taxon richness were positively correlated with sedimentary organic carbon and phaeophytin.

Chapter 4 is entitled, “A new species of *Polygordius* (Polychaeta: Polygordiidae): a dominant member of macrofaunal communities on the inner continental shelf and in bays and harbors of the northeastern United States” (Ramey et al. 2006). This research was motivated by frequent reports in ecological studies conducted along the northeast USA (including LEO-15) of a highly abundant, and often dominant undescribed species of polychaete. The goal was to describe this new species, including its 18S SSU rDNA sequence, and to provide information on its reproductive biology, circulatory system, habitat preferences, and ecological importance. It is the first North American *Polygordius* to be described and is distinguished from most other *Polygordius* species by its non-bulging, heavily ciliated pygidium, absence of pygidial glands, and the conical (rather than rounded) prostomium. This species thrives in sandy habitats in harbors, bays, and on the continental shelf to a maximum depth of 152 m on Georges Bank. Correlation of sediment grain size with density of *Polygordius jouinae* sp. nov showed that density was significantly ( $p = <0.05$ ;  $n=92$ ) positively correlated with the proportion of medium to very coarse sand and negatively correlated with the proportion of fine sand fractions.

Chapter 5 is entitled, “Life history of a dominant polychaete, *Polygordius jouinae*, in inner continental shelf sands of the Mid-Atlantic Bight, United States” (Ramey 2008, Marine Biology [accepted and resubmitted following minor revision]). Here the benthic phase of the life cycle of this ecologically important polychaete is characterized. Intensive seasonal sampling was conducted at LEO-15 from February 2004 to November 2005. Observations were made on reproductive mode, reproductive period, size at maturity, the number of generations in a population, and life span. *Polygordius jouinae* is gonochoristic and the ratio of sexually mature males to females is ~1:1. At LEO-15 the

population was mostly composed of sexually mature individuals in late May 2004 and 2005. The reproductive period occurred from May to August and spawning individuals have a one year life span. Recruitment begins no later than July as recently settled individuals ( $\leq 9$  mm body length), which were not present during the first week of June 1995, 2004, and 2005, first appeared in July in all three years. The smallest individual was 2.01 mm long and this provides the first estimate of size at initial recruitment.

Chapter 6 is entitled, “Selection by a dominant deposit-feeding polychaete, *Polygordius jouinae*, for sediments enriched with organic flocs” (Ramey and Bodnar 2008, Limnology and Oceanography [accepted and resubmitted following minor revision]). This chapter addressed whether subsurface migration and active selection by *P. jouinae* for elevated levels of sedimentary organic matter derived from organic-rich flocs explains small-scale patchiness of this species in sandy rippled beds. It was predicted that *P. jouinae* would detect and choose areas with relatively higher amounts of sedimentary organic matter in a directed manner (i.e., in response to some stimulus associated with the sedimentary organic matter). In a racetrack flume under realistic flow ( $u_* = 0.32 \text{ cm s}^{-1}$ ) and flat bed conditions, arrays of alternating fresh ambient sediment (+ organic) and freshly sieved sediment (-organic) showed significant subsurface movement of *P. jouinae* to sediment patches containing higher amounts of particulate organic matter (+ organic) in 48 h. Subsequent experiments showed that locating + organic patches was not the consequence of a directed search since *P. jouinae* did not detect favorable patches with higher amounts of organics at a 3-cm distance, even when patches were located upstream of the worm. However, worms that located + organic patches remained there and fed. Rate of movement in sediments indicated that *P. jouinae*



could potentially travel the wavelength of a typical ripple (14-30 cm) at LEO-15 in 35-75 min. Thus in a dynamic environment where food concentrations are low and patchy, the affinity of *P. jouinae* for particulate organic matter and its undirected, high rate of subsurface movement, is a plausible mechanism to account for the similar spatial distributions of this species and food resources in continental shelf sediments.

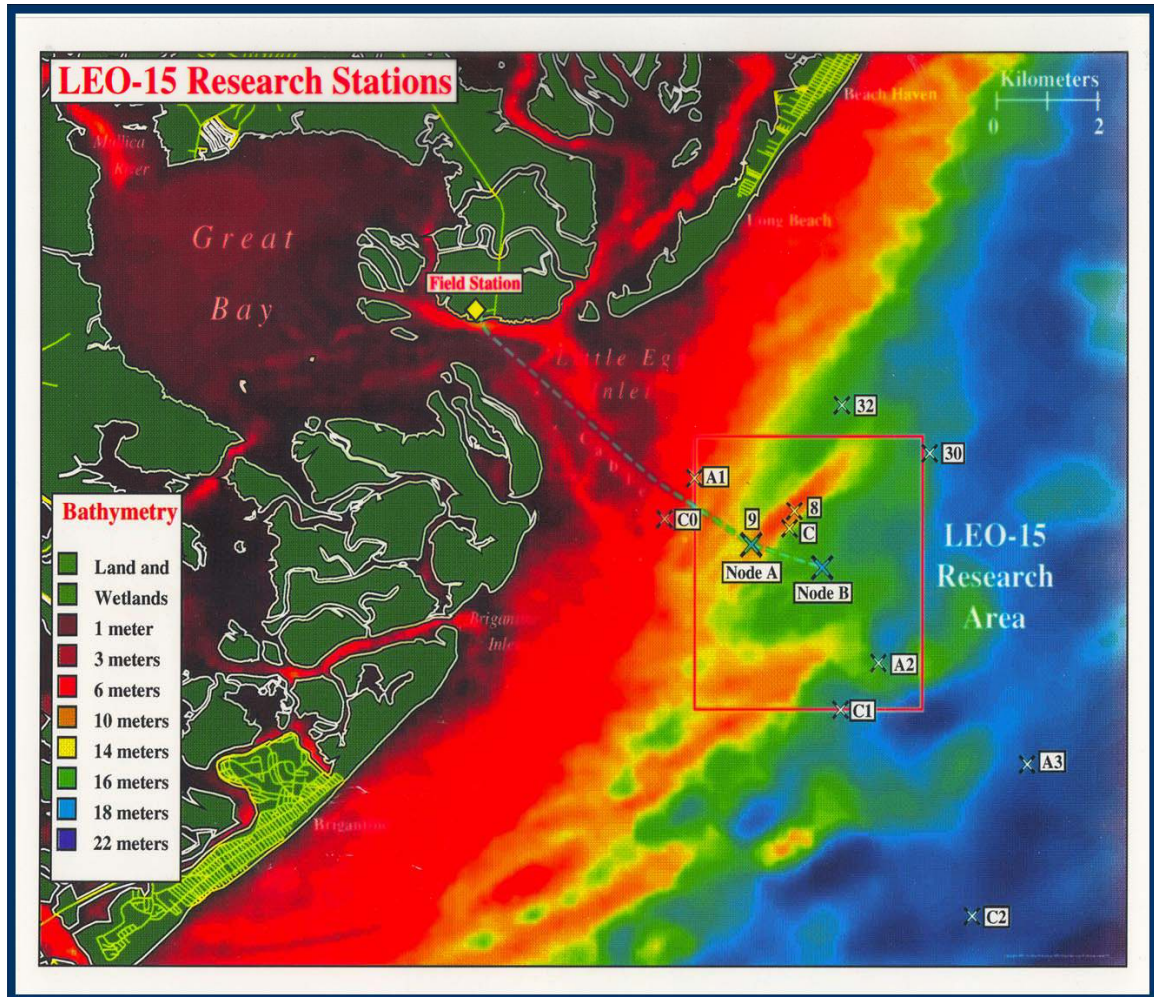


Fig.1.1: Bathymetry of Beach Haven Ridge at Rutgers University's Long-term Ecosystem Observatory at 15 m depth (LEO-15) on the inner continental shelf of southern New Jersey. LEO-15 area indicated by red square and bathymetry by colors. Underwater sampling nodes A or B provide a continuous stream of real-time data via underwater cable on the pressure, temperature, and salinity of the waters 1 m above the bed. LEO-15 research stations sampled in the present research included Stations 9 (southern landward side of ridge), 32 (northern landward side of ridge), and 30 (offshore flank of ridge). Other Stations referred to in this dissertation include Station 8 (ridge

crest), C (seaward of ridge), and C2 (offshore of ridge). Images from Rutgers University Remote Sensing Lab (RU-COOL).

## CHAPTER 2

### DO RIPPLE CRESTS AND TROUGHS SUPPORT DIFFERENT MACROFAUNAL COMMUNITIES?

#### INTRODUCTION

Distribution patterns of macro- and meiofaunal organisms (retained on 300- $\mu\text{m}$  and 63- $\mu\text{m}$  sieves respectively) in soft sediments are typically patchy in space and time (Eckman 1979; Morrissey et al. 1992). This patchiness is likely a reflection of the complexity of the sedimentary environment with which these organisms are intimately associated. This complexity is the result of physical (e.g., grain size, topographic features, hydrodynamics), chemical (e.g., organic matter, oxygen, trace metals) and biological (e.g., microbes, bioturbation, predators) environmental attributes (reviewed by Ólafsson et al. 1994; Snelgrove and Butman 1994) creating considerable habitat heterogeneity. Traditionally, macrofaunal community studies examining large-scale distribution patterns have broadly defined habitat based on sediment type (i.e., sand vs. mud) and grain size is considered to be one of the most important factors influencing patterns of diversity and abundance (Gray 1974; Etter and Grassle 1992). However, considerable patchiness also exists even when sediment grain size is homogeneous (e.g., Sandulli and Pinckney 1999) and relatively less is known about the variability of communities in the sandy sediments that cover approximately two-thirds of the continental shelf. Furthermore, these areas are often characterized by topographic features and biogenic structures that probably play a role in influencing spatial patterns of species distribution and abundance.

A  $\sim 3 \text{ km}^2$  area on the inner continental shelf off southern New Jersey constitutes the LEO-15 (Long-term Ecosystem Observatory at 15 m depth) research site ( $39^\circ 27.69' \text{ N}$ ,  $74^\circ 15.81' \text{ W}$ ) (Fig. 2.1). This area is dominated by Beach Haven Ridge, one shore-oblique sand ridge among 71 such ridges off the New Jersey coast (McBride and Moslow 1991). The ridge is  $\sim 5 \text{ km}$  long by  $1.5 \text{ km}$  wide, and has a maximum relief of  $8 \text{ m}$  between the ridge crest and trough on the shoreward side. Sediments in this area are primarily composed of well-sorted, medium to coarse sands with a median grain size of  $400\text{-}500 \text{ }\mu\text{m}$  (Reimers et al. 2004). Sediments are coarsest near the base of the landward flank of the ridge and become progressively finer as one moves up the flank and down the seaward side (Craghan 1995). Although temporal changes in mean grain sizes occur at certain locations on the ridge, these changes are not extreme, meaning that grain sizes become moderately coarser or moderately finer within the constraints of this general pattern (Craghan 1995). Like other physically active shelf areas, rippled beds are the predominant habitat feature (Able et al. 2003).

The present study examined macrofaunal community patterns at two stations at LEO-15 with relatively similar coarse sandy sediments and rippled beds. One station was located inshore on the southern landward side of the ridge at  $\sim 12 \text{ m}$  depth (Sta. 9), and the other was located offshore of the ridge at  $16 \text{ m}$  depth (Sta. 30),  $\sim 4 \text{ km}$  northeast of the inshore station. Comparison of sediment grain size between these two stations in 1990 indicated that they were relatively similar, with slightly coarser sediments offshore at Sta. 30 (mean grain size Sta. 9:  $500 \text{ }\mu\text{m}$  [ $\Phi=1.0$ ]; Sta. 30:  $\Phi=0.9$ ) (Craghan 1995). In June 2005, sediments at Sta. 30 were composed of a much higher percent of coarser grained sediment ( $\geq 500 \text{ }\mu\text{m}$ :  $72.6 \pm 2.5$ ) than medium to finer grained sediment ( $< 500 \text{ }\mu\text{m}$ :  $27.4$

$\pm 2.5$ ) (Schmidt, unpubl.). At Sta. 9 in June 2006, sediments had a higher percentage of medium to finer grained sediment ( $< 500 \mu\text{m}$ :  $62.0 \pm 22.5 \%$ ) than coarser grained sediment ( $\geq 500 \mu\text{m}$ :  $29.6 \pm 14.9 \%$ ) (Ramey, unpubl.).

Sediments at LEO-15 are frequently in motion due to waves, storms, and stronger than average currents. This movement creates a rippled bed with varying heights and wavelengths over space and time. Sediment transport is driven by waves with both onshore and offshore components. Sand grains move shoreward with the wave crest and seaward with the passing of the wave trough creating symmetrical ripples with sharp crests. During a particularly active period from August to September 1995, mean alongshore currents (measured 44 cm above the bottom) near Sta. 9 were 5 to 20  $\text{cm s}^{-1}$  and cross-shore currents associated with the tides were generally  $\leq 8 \text{ cm s}^{-1}$  (Traykovski et al. 1999). During this same period, ripple heights ranged from 3 to 15 cm and wavelengths from 10 to 100 cm (Traykovski et al. 1999). More recently, Newby (2006) reported heights of 3 to 4 cm and wavelengths of 14 cm in late November 2004 at Sta. 9 and by mid-May 2005, ripple heights at this site had increased to 10 cm and wavelengths to  $\sim 38$  cm. Similar data are unavailable for Sta. 30.

As ripple crests form, low density organic fines and mineral grains are winnowed out of crests and deposited in troughs (Reimers et al. 2004). Moreover, unidirectional and oscillating bottom flows can interact with the rippled bed to create localized pressure differences or interstitial fluid advection (Huettel and Gust 1992). This process is unique to permeable sediments, such as those at LEO-15. Near bottom water containing particulate organic matter (POM) and oxygen, is pumped into the sediments in ripple troughs, where POM may become trapped, whereas pore water is pumped out at the apex

of crests (Huettel et al. 1996; Ziebis et al. 1996). This creates considerable environmental heterogeneity and may offer infauna different physical environments and food resources (Sedlacek and Thistle 2006).

Several studies have found different densities of benthic organisms inhabiting crests than troughs (e.g., Sameoto 1969; Grant 1981; Barros et al. 2004) suggesting that these topographic habitat features may be an important source of microhabitat specialization in physically active sedimentary environments (Hogue and Miller 1981). The primary goal of the present study was to examine whether crests and troughs of sand ripples in two areas with moderate differences in sediment grain sizes, support different macrofaunal communities and to determine whether the observed patterns change over space and time. Specific questions asked were: 1. Do macrofaunal communities inhabiting crests of ripples differ from those in troughs?; 2. Can observed community patterns (i.e. species composition and abundance) be related to spatial scale (m to km)?; 3. What species are most important in driving observed differences in community structure?; 4. Are community patterns and species driving them consistent over time (i.e., sampling dates).

## MATERIALS AND METHODS

### Sampling design

Sediment cores (7-cm diameter, 10 cm deep, 38.5 cm<sup>2</sup>) were collected by SCUBA divers using a hand held corer at LEO-15. Samples were taken on 20 July 1994, 20 September 1994, 14 November 1994, 5 June 1995, and 12 October 1995 from two stations with sandy rippled beds, about 4 km apart. Station 9 (12-m depth) is located on

the inshore side of Beach Haven Ridge, and station 30 (16-m depth) on the offshore flank (Fig. 2.1). A nested, partially randomized sampling design (habitat specified: crest or trough) was used where within each station (each station: 200-m diameter), three 60-m diameter areas called “substations” were set up, and within each of these a pair of macrofaunal samples including one from a crest and the other from a trough, were collected at three points (6 cores [3 crests and 3 troughs]  $\text{substation}^{-1}$  = 18 cores  $\text{station}^{-1}$ ;  $n$  = 180 cores over all dates sampled), (Fig. 2.2.). Substation locations were randomly chosen within a 100-m radius of the approximate center of each station. This was determined by generating random compass bearings and distances of 0-360° and 0-100 m respectively. These values were then used to calculate substation co-ordinates (i.e., latitude and longitude) originating from the initial center of each station. Thus, each substation location lay in a random direction at a random distance from the original station. Sampling points were randomly chosen within a 30-m radius of each substation location as outlined above, except that map co-ordinates were obtained relative to the substation co-ordinates. Thus, the two stations were ~4 km apart, the three substations were  $\leq 200$  m apart, and the three sampling points where paired crest and trough samples were taken were  $\leq 60$  m apart. Samples were sieved over a 300- $\mu\text{m}$  mesh screen, fixed in 10% formalin/seawater mixture, and then promptly transferred to 70% ethanol with rose bengal. Macrofauna were identified to the lowest possible taxonomic level (generally genus or species) where possible. In some cases, small juveniles could not be identified and were grouped by Family or some higher level of classification and referred to as spp.



### Data Analysis

Community composition analysis was compared among stations, dates, and ripple crest and trough habitats on individual macrofaunal cores (i.e. cores were not averaged or pooled) using CNESS (Chord Distance Normalized Expected Species Shared) as described by Trueblood et al. (1994). This analysis was performed on the entire data set (i.e. including species and samples from both stations and all dates sampled) and then separate analyses were conducted for each sampling date. CNESS is a faunal index based on an extension of Orlóci's (1978) and Grassle and Smith's (1976) NESS (Normalized Expected Species Shared). CNESS produces a dissimilarity matrix from a sample x species matrix, and is based upon the number of expected species shared in a random draw of  $n$  individuals ( $n=10$ ) from two samples. This particular index was chosen because it is sensitive to rare as well as abundant species. To provide a more comprehensive and informative presentation of the data, a metric scaling of CNESS was performed in Matlab programs written by Dr. Eugene D. Gallagher, UMASS/Boston (see <http://alpha.es.umb.edu/faculty/edg/files/edgwebp.htm>). The metric scaling of CNESS converts the sample-by-species matrix to a normalized hypergeometric probability matrix (H), which describes the probability of sampling each species in each sample with a random draw of 10 individuals. This hypergeometric matrix is then analyzed by Principal Components (PCA-H). The first two scores from the PCA-H provide a two dimensional metric scaling of CNESS distances among samples representing the best least-squares fit for the data. This plot is very similar to that produced by non-metric multidimensional scaling (NMDS) (Trueblood et al. 1994; Snelgrove et al. 2001), but the advantage of the metric scaling is that CNESS distances among samples are preserved. Thus species that

contribute to CNESS variation among samples can then be displayed in a Gabriel Euclidean distance biplot overlay (Gabriel 1971; Ter Braak 1983), where the length and angle of species vectors indicate the contribution of the species to the PCA-H axes. For simplicity, only species that contributed >5% to CNESS variation were included in the biplots.

Average densities of species shown to be influential in creating the spatial pattern from the biplots were compared among ripple crests and troughs by plotting means with 95% confidence intervals for each sampling date and station. Summary variables including density of total macrofauna, richness, Shannon-Wiener diversity  $H'$  (base 2), and evenness  $J'$  were also compared in the same manner. To determine whether there were significant differences in any of these measures in ripple crests and troughs both within and between the two stations a non-parametric test (Mann-Whitney U) was performed in SPSS.

## RESULTS

A total of 43,708 individuals were collected encompassing 140 different taxa. Core sample groupings based on PCA-H analysis of all macrofaunal cores showed that samples taken on the same date tended to group together and temporal patterns were similar between the two stations (Fig. 2.3). The most distinct group was composed of samples collected in July 1994 at Sta. 30 (Fig. 2.3B). Samples from June 1995 and October 1995 were very similar to each other and formed another group (Fig. 2.3). In contrast, November samples showed considerable overlap with those from other dates (Fig. 2.3).

Sample groupings produced from PCA-H analysis of macrofaunal cores for each sampling date revealed groups that were not evident in the former analysis. Depending on date, discernible communities were present between stations (Sta. 9 and Sta. 30) and habitats (i.e. crests or troughs). It must be noted, however, that there were always a few samples that did not follow these patterns. Samples generally grouped by station in July 1994 and October 1995 (Figs. 2.4A, 2.5A, 2.8A) and by habitat in July 1994, September 1994, November 1994, and June 1995 (Figs. 2.4A-2.6A). To a lesser degree macrofaunal cores were also arranged, spatially by substation (i.e., 3 substations located  $\leq 200$  m apart) and sampling point (i.e., 3 sampling points located  $\leq 60$  m apart) (Figs. 2.4B-2.7B), (e.g., Fig 4B, Sta. 9).

In general, macrofaunal communities in paired crest and trough samples (spatial scales of  $<1$  m) were more different from each other than from crest or trough samples taken further away (60 to 200 m). This pattern, which was consistent at stations 9 and 30 on four out of five sampling dates, reflects considerable within-station variation in macrofaunal assemblages. Moreover, communities were more similar among crest samples and among trough samples (scales of m to 4 km), than between paired crest and trough samples ( $< 1$  m) collected from their respective stations on three of the five sampling dates (i.e., September 1994, November 1994, and June 1995). The only exception to these patterns occurred at both stations in the 12 October 1995 samples.

Comparisons of community related variables among stations indicated total macrofaunal density and taxon richness were significantly greater at Sta. 30 compared to Sta. 9 in ripple crests (total density:  $\bar{x} = 175.9$  ind.  $38.5 \text{ cm}^{-2}$  Sta. 30 vs  $\bar{x} = 109.2$  ind.  $38.5 \text{ cm}^{-2}$  Sta. 9; richness:  $\bar{x} = 18.2$  Sta. 30 vs  $\bar{x} = 14.4$  sta. 9) as well as in troughs (total

density:  $\bar{x} = 342.4$  ind.  $38.5 \text{ cm}^{-2}$  Sta. 30 vs  $\bar{x} = 188.2$  ind.  $38.5 \text{ cm}^{-2}$  Sta. 9; richness  $\bar{x} = 19.4$  Sta. 30 vs  $\bar{x} = 15.5$  Sta. 9) (Table 2.1, Fig 2.9A-D). Shannon diversity ( $H'$ ) and evenness did not differ significantly among stations (Table 2.1; Fig. 2.9 E-H). In terms of habitat, total density of macrofauna was significantly greater in troughs than in crests at both stations (Sta.30:  $\bar{x} = 342.4$  ind.  $38.5 \text{ cm}^{-2}$  troughs vs  $\bar{x} = 175.9$  ind.  $38.5 \text{ cm}^{-2}$  crests; Sta. 9:  $\bar{x} = 188.2$  ind.  $38.5 \text{ cm}^{-2}$  trough vs  $\bar{x} = 109.2$  ind.  $38.5 \text{ cm}^{-2}$  crest) (Table 2.1; Fig. 2.9A-B). Although taxon richness was also generally higher in troughs relative to crests at both stations these differences were not significant (Table 2.1; Fig. 2.9C-D). Shannon diversity and evenness showed the opposite trend and were significantly higher in crests than in troughs at both stations and at Sta. 30 respectively (Table 2.1; Fig. 2.9E-H).

More specifically, a total of 13 taxa including 8 polychaetes, 3 bivalves, *Oligochaeta* spp., and *Nemertea* spp. were identified in Gabriel biplots as being important in distinguishing among the sample groupings identified by the PCA-H analysis of macrofaunal cores for each sampling date, described above (Table 2.2; Figs. 2.4A-2.8A). Depending on the date examined, different combinations of these taxa were important in creating the observed patterns (3-6 taxa per date) (Table 2.2). Most taxa (7 out of 13) were important in distinguishing among groups on a single date. The polychaete, *P. jouinae*, surfclam *S. solidissima*, and *Nemertea* spp., however, were important on at least three of the five dates examined. *Polygordius jouinae* contributed to between-station variation in July 1994 and October 1995, and between-habitat variation in July 1994, November 1994, and June 1995. In July, density of *P. jouinae* was significantly greater at Sta. 9 compared to Sta. 30 in ripple crests (Sta. 9:  $\bar{x} = 9.0$  ind.  $38.5 \text{ cm}^{-2}$  vs Sta. 30:  $\bar{x} = 0.0$  ind.  $38.5 \text{ cm}^{-2}$  vs) as well as in troughs (Sta. 9:  $\bar{x} = 26.4$  ind.  $38.5 \text{ cm}^{-2}$  vs Sta. 30:  $\bar{x} =$

0.11 ind. 38.5 cm<sup>-2</sup>) (Table 2.3; Fig. 2.10). In October this pattern was reversed and density was greater at Sta. 30 compared to Sta. 9 but this difference was not significant (Table 2.3; Fig. 2.11). In terms of habitat, density of *P. jouinae* was significantly greater in troughs than in crests at station 9 in July ( $\bar{x}$  = 26.4 ind. 38.5 cm<sup>-2</sup> troughs vs  $\bar{x}$  = 9.0 ind. 38.5 cm<sup>-2</sup> crests), at both stations in November 1994 (Sta. 30:  $\bar{x}$  = 351.9 ind. 38.5 cm<sup>-2</sup> trough vs  $\bar{x}$  = 46.3 ind. 38.5 cm<sup>-2</sup> crest; Sta. 9: 142.7 ind. 38.5 cm<sup>-2</sup> trough vs  $\bar{x}$  = 46.3 ind. 38.5 cm<sup>-2</sup> crest), and at station 30 in June 1995 ( $\bar{x}$  = 93.3 ind. 38.5 cm<sup>-2</sup> trough vs  $\bar{x}$  = 23.8 ind. 38.5 cm<sup>-2</sup> crest), (Table 2.3; Figs. 2.10, 2.12, 2.14). Density was also greater in troughs than in crests in June at station 9 but this difference was not significant (Fig. 2.13). *Spisula solidissima* contributed to between-station variation in July 1994, September 1994, and October 1995, and between-habitat variation in July 1994, and September 1994. In July and September 1994, density of this clam was significantly greater at Sta. 9 than at Sta. 30 in both ripple crests and troughs (Table 2.3; Figs. 2.10, 2.13). Density differences between Sta. 9 and Sta. 30 on 12 October 1995 were negligible (Table 2.3; Fig. 2.10). In contrast to *P. jouinae*, density of *S. solidissima* was highly variable between crests and troughs depending on station and date. For example, at both stations in July 1994, density was greater in crests than troughs, but this difference was only significant at Sta. 30 (Table 2.3; Fig. 2.10). In contrast, in September 1994 density was significantly greater in troughs than in crests at both stations (Table 2.3; Fig. 2.13). This was also the case at Sta. 9 in October but this difference was not significant (Table 2.3; Figs. 2.11). Density of Nemertea spp. contributed to within-station community variation in September 1994, November 1994, and June 1995 and density was consistently higher in crests than in troughs. Density patterns among stations and habitats

along with statistics for the other species identified in Gabriel biplots are shown (Table 2.3; Figs. 2.10-2.14).

## DISCUSSION

This study examined community assemblages associated with different topographic habitat features (i.e., ripple crests and troughs) at multiple spatial scales (m to km) in relatively homogeneous sandy sediments over time. Community differences (i.e., species composition and abundance) were most pronounced among sampling dates, however, when only a single date was considered, differences were related to ripple crest and trough habitats. Further variation, beyond that of habitat, was attributed to the largest spatial scale (between stations; 4 km apart), whereas, community patterns at spatial scales of 60 to 200 m were diffuse and inconsistent. Different combinations of taxa were found to be important in driving these patterns depending on sampling date. Given the diversity of reproductive strategies, feeding modes, food preferences, and motility of taxa it is not surprising that taxa exhibit different habitat associations and patterns. The only date where communities did not differ between crests and troughs was October when samples were collected following a particularly stormy, 2-week period at the end of September (J. Grassle, pers. comm.). Along the east coast, more hurricanes and Northeasters generally occur from November to April every year, with less storm activity from May to October (Zhang et al. 2001). Such storms result in substantial sediment resuspension and transport, disrupting community patterns established in crests and troughs during calmer periods.

In concert with my findings, Barros et al. (2004) also found less variability in macrofaunal communities (500  $\mu\text{m}$  sieve; Family level identification) from replicate to replicate within crests and within troughs than between crests and troughs (scales of  $\leq 4\text{m}$  to 10 m) in Botany Bay, Australia at 7-8 m depth. Abundances of infauna inhabiting crests have been described as different from those in troughs in high-energy subtidal (e.g., nematodes: Sameoto 1969; macrofauna 500-  $\mu\text{m}$  sieve: Barros et al. 2004) and intertidal sandy sediments (crustaceans: Grant 1981) with some having significantly higher abundances in troughs than crests (Barros et al. 2004) and vice versa (Grant 1981). Community differences between crests and troughs at LEO-15, irrespective of station, were driven by differences in the relative abundance of three dominant taxa including *Polygordius jouinae*, *Spisula solidissima*, and nemerteans (i.e., *Nemertea* spp. and *Nemertea* sp.A). Density of *P. jouinae* was consistently higher in troughs than in crests at both stations. In contrast *S. solidissima* was highly variable between crests and troughs depending on station and date, and density of *Nemertea* spp. was higher in crests. Macrofauna may be passively transported to (via resuspension and beadload transport) and deposited in troughs (Eckman 1979). Additionally, several studies have suggested that active selection by post-larval stages may also be responsible for distribution patterns associated with crests and troughs (e.g., Sameoto 1969; Grant 1981). At LEO-15 a combination of these factors may be important in influencing distributions of macrofauna between crests and troughs; a topic of further research in subsequent chapters (e.g., active habitat selection, Chapter 6).

*Polygordius jouinae* is an interstitial, deposit-feeding polychaete, the reproductive period for this species at LEO-15 occurs from May to August, and spawning individuals

have a one-year life span (Ramey, in revision; also see Chapter 5). Thus, the population was generally composed of mature adults in May and June, and recently settled juveniles entered the population, with a corresponding decrease in sexually mature adults, no later than July (Ramey, in review; and Chapter 5). The higher density of *P. jouinae* in troughs than in crests at LEO-15 was investigated by Ramey and Bodnar (in revision; also see Chapter 6) and might be established by an interaction between the behavior of *P. jouinae* and the effects of unidirectional near bottom flows on the distribution and concentration of particulate organic matter within trough sediments. Patches of fine organic flocs have been observed by divers on the surface of ripple troughs at LEO-15 (Petrecca, pers. comm.) and sedimentary particulate organic matter was significantly higher in ripple troughs than in crests in samples collected at Sta. 9, June 2005 (see Chapter 3). Flume experiments showed that under realistic flow (free stream velocity of  $5 \text{ cm s}^{-1}$ ;  $u_* = 0.32 \text{ cm s}^{-1}$ ; Styles 1998) and flat bed conditions, adult *P. jouinae* selected for higher levels of particulate organic matter, and observations on rates of movement in sediments indicated that worms could potentially travel the wavelength of a typical ripple (14-30 cm) at LEO-15 in 35-75 min (Ramey and Bodnar, in revision; and Chapter 6). Several experimental studies, unrelated to rippled beds, have shown that juvenile and adult macrofaunal species actively leave sediments in response to low or depleted food resources such as organic matter (polychaetes: Olivier et al. 1996; Stocks 2002; Oligochaetes: Nilsson et al. 2000).

There is also some evidence for post-larval selection, and passive or active transport via re-suspension or bedload by *P. jouinae* at LEO-15. A reciprocal sediment transplant experiment conducted by Snelgrove et al. (1999) showed *P. jouinae* selected sandy sediments (Sta. 9) over muddy sediments (Sta. 32) in hydrodynamically unbiased



trays, placed in troughs for 3 to 5-d, and Ramey (in review; and Chapter 5) found that the majority of these worms were juveniles. Since experimental sediment trays precluded movement through the sediment by worms, it is probable that they were passively or actively transported into trays from surrounding sediments. It may be that juvenile *P. jouinae* concentrated in the upper sediment layer are more easily resuspended than adults living deeper in the sediment. A preliminary experiment in the racetrack flume (modeled after Stocks 2002) lends support for passive transport of this worm. Very few adult *P. jouinae* actively emerged from inorganic sediments over 18 h, at a free stream velocity ( $18 \text{ cm s}^{-1}$ ) that did not cause sediment transport (Ramey and Ballew, unpubl.).

Larval and post-larval transport and selection have also been found to be important in influencing distribution patterns of the surfclam *S. solidissima* at LEO-15. Larval and juvenile *S. solidissima* selected sandy sediments over muddy sediments in Snelgrove et al.'s (1999) reciprocal sediment tray experiments and sampling date significantly influenced larval settlement intensity over a 6-week period in the summer. However, unlike *P. jouinae*, distribution patterns between crests and troughs for the surfclam *S. solidissima* were inconsistent between stations and among sampling dates. Newby (2006) also reported inconsistent patterns in distribution of *S. solidissima* between crests and troughs at LEO-15 (Sta. 9 and 8). Inconsistent patterns may result from differences in susceptibility of individual *S. solidissima* to re-suspension or bedload transport, and to migration of ripples over clams able to avoid erosion by burrowing deeper in the sediment. *Spisula solidissima* is a suspension feeder and the need to remain in sediments with relatively higher levels of sedimentary organic matter is probably much less important than for *P. jouinae*. Moreover, juvenile *S. solidissima* are restricted to

surface sediments due to their short siphon length (Zwarts and Wanink 1989) which makes them susceptible to re-suspension and bedload transport as well as predation. Flume experiments have shown that vertical burrowing behavior of juvenile *Mya arenaria* (< 2 mm shell length) reduced the number of individuals eroded from the sediment as sediment movement was initiated (Roegner et al. 1995; Hunt 2004). However, as shear velocities increased, they were unable to keep pace with sediment erosion and were transported downstream. More specifically, Newby (2006) conducted flume experiments to examine the ability of juvenile *S. solidissima* to avoid erosion via burrowing behavior in migrating ripples (height ~3.0 cm; wavelength ~13-16 cm; migration rates 7.3 to 26.8 cm h<sup>-1</sup>). Surfclams did not move with migrating ripples. Instead, they either remained in the initial patch where they were placed or were transported varying distances downstream where they were deposited in a trough and sub-sequently re-entered the sediments (Newby 2006).

Densities of nemerteans were consistently higher in ripple crests than troughs in the field sampling at Sta. 9 and 30. Most nemertean species prey on live marine invertebrates (e.g., crustaceans and polychaetes) and many species show strong preferences for particular prey items (Thiel and Kruse 2001). Higher densities observed in crests than in troughs may be related to density differences of preferred prey species. For example, predatory amphipods have been observed to occur in higher abundances beneath ripple crests associated with their meiofaunal prey (Fenwick 1984). Although several species of amphipods were present in crests and troughs at LEO-15, densities were low and were not generally higher in crests than in troughs. It may be that the

Nemertea spp. at LEO-15 feed on smaller meiofaunal crustaceans such as copepods and further research is necessary to understand their association with ripple crests.

Community differences at the largest scale between the inshore Sta. 9 and offshore Sta. 30 (4 km apart) occurred on two of the five dates examined. The relative abundances of taxa including *S. solidissima*, *P. jouinae*, and *Syllides convoluta*, rather than any single species having a strict affinity with one station or the other, distinguished the communities at stations 9 and 30 in July 1994 and October 1995. The exceptions to this were *Oligochaeta* spp., and *Peosidrilus* spp., which only occurred at Sta. 30 in October. Most notably, differences between Sta. 9 and 30 corresponded with seasons when larval settlement and recruitment for many macrofaunal species is maximal at LEO-15 (Ma and Grassle 2004; J. Grassle, pers. comm.). Thus, community differences between inshore Sta. 9 and offshore Sta. 30 may have been a result of larger scale factors such as circulation patterns, upwelling and downwelling events, combined with differences in life history strategies, all of which can differentially influence larval supply and settlement at these two locations.

Most support for this comes from long-term studies (1993-2004), at LEO-15 for *S. solidissima* which have shown considerable variability in larval supply and settlement to and divergence among inshore and offshore stations at LEO-15 in June, July, and October when settlement is maximal (Ma 2005; Ma et al. 2006; Snelgrove et al. 1999; Snelgrove et al. 2001; Weissberger and Grassle 2003). Spatial and temporal variations in larval supply have been shown to be controlled by upwelling and downwelling circulation during summer months, and settlement was in turn influenced by larval supply. Recurring patterns resulting from inshore spawning populations in July indicate

relatively higher larval supply and settlement of *S. solidissima* inshore at Sta. 9 than offshore at Sta. C2 (Ma 2005; Ma et al. 2006). A second recruitment pulse occurs in October or November as a consequence of spawning populations offshore, under the influence of the Middle Atlantic cold pool, which spawn when the thermocline breaks down in the late summer or early fall (or in some instances when there is storm mixing) (Ma et al. 2006). Fall-spawned larvae are thought to be widely dispersed on the continental shelf and settlement patterns between inshore Sta. 9 and offshore Sta. C2 in October and November have been shown to be the same as those observed for inshore spawning populations in July (Ma et al. 2006). The already mentioned reciprocal sediment tray experiments (Snelgrove et al. 1999) also demonstrated that differences in larval supply over scales of kilometers and time scales of weeks can affect settlement intensity inshore at stations 9 and 32 at LEO-15.

Given the similarity between *S. solidissima* and *P. jouinae* in timing of spawning and summer settlement, it is likely that these same processes were important in influencing the higher density of *P. jouinae* inshore at Sta. 9 compared to offshore Sta. 30 in July. The relatively large numbers of small eggs (1000's; diameter <63  $\mu\text{m}$ ) and sperm structure in *P. jouinae* indicate free spawning with planktotrophic larvae (Ramey et al. 2006; and Chapter 4). As mentioned above, the reproductive period for this species at LEO-15 generally occurs from May to August with settlement beginning no later than July (Ramey et al. 2006; and Chapter 5). The higher density of this species at Sta. 30 compared to Sta. 9 in October 1995 may simply have been due to differences in larval supply and recruitment between the two years. There is little evidence in support of a

second recruitment pulse for *P. jouinae* in the fall at inshore stations (Ramey et al. 2006; and Chapter 5), however, offshore populations of this species have not been studied.

Higher densities of the interstitial polychaete, *Syllides convoluta*, occurred offshore at Sta. 30 than inshore at Sta. 9 in July and October. In general, brooding with direct development of a relatively small number of eggs is prevalent in the genus *Syllides* (Giangrande 1997; Franke 1999) and reproduction likely occurs more than once a year. Higher densities in July and October at Sta. 30 could correspond with a spring and fall reproductive period for this species, but the size distributions of these samples are unknown. Dispersal ability of brooding species is generally thought to be relatively restricted, compared with those species with planktonic larvae such as *P. jouinae* and *S. solidissima*, which may help explain the localized distribution and abundance patterns of *S. convoluta*.

Finally, one cannot rule out the possibility that differences in the type and abundance of predators inshore at Sta. 9 and offshore at Sta. 30 may also contribute to observed community patterns, following settlement pulses in July 1994 and October 1995. Weissberger and Grassle (2003) found that some predators, including the moon snail *Neverita duplicata* and several crab species, settled more or less simultaneously with *S. solidissima*. Moreover, studies have shown that a rapid reduction in the number of recently settled surfclams occurs within a few weeks after larval settlement (Weissberger and Grassle 2003; Ma et al. 2006; Quijon and Grassle 2007 prep.). However, it may be that predators play a greater role in reducing differences between stations than in creating them. For example, Quijon et al. (2007) found naticid predation consistently contributed to a reduction of spatial differences in density of *S. solidissima* between Sta. 9 on the

shoreward side of the ridge and Sta. C on the seaward side, which were initially created by dissimilar levels of larval settlement. In the present study, following settlement in July 1994 and October 1995, communities in September 1994, November 1994 and June 1995 were relatively more similar to each other, and *S. solidissima* was not important in influencing observed patterns in November 1994, and June 1995.

## CONCLUSIONS

These results highlight the fundamental influence small-scale differences in topographic habitat features can have on macrofaunal species distributions and abundances in sandy continental shelf sediments. Such features should be considered in future sampling designs when patterns of distribution are examined. Community differences (i.e., species composition and abundance) were most pronounced among sampling dates, however, when only a single date was considered, differences were related to ripple crest and trough habitats. Community differences between ripple crests and troughs, irrespective of station, were driven by differences in the relative abundance of three dominant taxa including *Polygordius jouinae*, *Spisula solidissima*, and nemerteans. In July and October, further variation, beyond that of habitat, was attributed to the largest spatial scale (4 km) between the inshore and offshore stations, which corresponded with seasons when larval recruitment for many macrofaunal species is maximal at LEO-15. Here, the relative abundances of taxa (i.e., *S. solidissima*, *P. jouinae*, and *Syllides convoluta*), rather than any single species having a strict affinity with one station or the other, distinguished communities. Communities did not differ between stations during times of the year following peak settlement such as in September 1994,

November 1994, and June 1995. Previous research at LEO-15 suggests that a combination of passive re-suspension, bedload transport, and active habitat selection may be important in influencing smaller scale community patterns, such as those observed here in rippled beds. On the other hand, community patterns at larger scales between inshore and offshore stations may result from circulation in the vicinity of Beach Haven Ridge, upwelling and downwelling events, combined with differences in life history strategies, all of which can differentially influence larval supply and settlement at these two locations.

Table 2.1: Summary of the 13 taxa/species contributing to >5 % of CNESS variation among samples and displayed in Gabriel Euclidean distance biplots. + indicates taxon contributed to variation on a particular sampling date (i.e. July 1994, September 1994, November 1994, June 1995 and October 1995).

Group	Taxa/species	20 Jul. 1994	20 Sep. 1994	14 Nov. 1994	5 Jun. 1995	12 Oct. 1995
Polychata	<i>Polygordius jouinae</i>	+		+	+	+
	<i>Tharyx acutus</i>	+				
	<i>Tharyx kirkegaardi</i>	+	+			
	<i>Syllides convoluta</i>	+				+
	<i>Aricidea catherinae</i>				+	
	<i>Caulleriella</i> sp. A					+
	Spionidae juv sp. A			+		
Bivalvia	<i>Spisula solidissima</i>	+	+			+
	<i>Nucula annulata</i>				+	
	<i>Tellina</i> spp.				+	
Oligochaeta	<i>Peosidrilus</i> spp.					+
Nemertea	<i>Nemertea</i> spp.		+	+	+	
	<i>Nemertea</i> sp. A		+		+	



Table 2.2: Mann-Whitney test for differences in total density, taxon richness, diversity, and evenness among stations (i.e., in Sta. 9 crests vs. Sta. 30 crests and Sta.9 troughs vs. Sta. 30 troughs) and among habitats (i.e., crests vs. troughs at Sta. 9 and crests vs. troughs at Sta. 30) at  $\alpha=0.05$ . Mann-U values are given to the left of / and p-values to the right. Significant p-values indicated with \* and bolded.

Variables	Station		Habitat	
	Sta. 9 vs. 30 (crest; $n=90$ )	Sta. 9 vs. 30 (trough; $n=90$ )	Crest vs. trough (Sta. 9; $n=90$ )	Crest vs. trough (Sta. 30; $n=90$ )
Total density	673.5 / <b>0.006</b> *	632.5 / <b>0.003</b> *	738.0 / <b>0.027</b> *	640.0 / <b>0.004</b> *
Richness	553.0 / <b>&lt;0.001</b> *	656.5 / <b>&lt;0.001</b> *	877.0 / 0.273	860.0 / 0.285
Diversity H' (base 2)	800.0 / 0.086	979.0 / 0.0928	744.0 / <b>0.030</b> *	684.0 / <b>0.012</b> *
Evenness J'	984.0 / 0.818	806.5 / 0.132	806.0 / 0.096	657.0 / <b>0.006</b> *

Table 2.3: Mann-Whitney test for differences in density of taxa among stations (i.e., at Sta. 9 crests vs. Sta. 30 crests and Sta. 9 troughs vs. Sta. 30 troughs) and among habitats (i.e. crests vs. troughs at Sta. 9 and crests vs. troughs at Sta. 30) at  $\alpha=0.05$  for taxa contributing to >5 % of CNESS variation among samples and displayed in Gabriel Euclidean distance biplots for each sampling date (i.e. July 1994, September 1994, November 1994, June 1995, and October 1995). Mann-U values are given followed by p-values. Significant p-values indicated in bold with \*.

Date	Species	Station Sta. 9 vs. 30 (crest; $n=18$ )	Sta. 9 vs. 30 (trough; $n=18$ )	Habitat Crest vs. trough (Sta. 9; $n=18$ )	Crest vs. trough (Sta. 30; $n=18$ )
20 Jul. 1994	<i>Polygordius jouinae</i>	0.00 / < <b>0.001</b> *	0.00 / < <b>0.001</b> *	10.0 / <b>0.006</b> *	36.0 / 0.730
	<i>Tharyx acutus</i>	40.0 / 1.00	25.5 / 0.190	32.5 / 0.489	16.0 / <b>0.031</b> *
	<i>Tharyx kirkegaardi</i>	38.5 / 0.863	39.0 / 0.931	32.5 / 0.489	24.5 / 0.161
	<i>Syllides convoluta</i>	7.50 / <b>0.002</b> *	37.0 / 0.796	39.5 / 0.931	10.0 / <b>0.006</b> *
	<i>Spisula solidissima</i>	2.50 / < <b>0.001</b> *	7.50 / <b>0.002</b> *	29.0 / 0.340	17.5 / <b>0.040</b> *
20 Sep. 1994	<i>Tharyx kirkegaardi</i>	39.5 / 0.931	27.5 / 0.258	22.0 / 0.113	27.5 / 0.258
	<i>Spisula solidissima</i>	12.5 / <b>0.011</b> *	4.50 / < <b>0.001</b> *	13.0 / <b>0.014</b> *	4.50 / < <b>0.001</b> *
	Nemertea spp.	25.0 / 0.190	24.0 / 0.161	24.5 / 0.161	24.0 / 0.161
	Nemertea sp. A	12.5 / <b>0.011</b> *	37.5 / 0.796	36.0 / 0.730	37.5 / 0.796
14 Nov. 1994	<i>Polygordius jouinae</i>	40.0 / 1.0	23.0 / 0.236	7.00 / <b>0.002</b> *	15.5 / <b>0.046</b> *
	Spionidae juv. Sp. A	31.5 / 0.436	13.5 / <b>0.027</b> *	40.5 / 1.0	24.5 / 0.277
	Nemertea spp.	26.5 / 0.222	22.0 / 0.200	22.0 / 0.113	22.5 / 0.200
5 Jun. 1995	<i>Polygordius jouinae</i>	33.0 / 0.546	19.0 / 0.063	26.5 / 0.222	13.0 / <b>0.014</b> *
	<i>Aricidea catherinae</i>	28.5 / 0.297	26.0 / 0.222	37.0 / 0.796	40.0 / 1.0
	<i>Nucula annulata</i>	30.0 / 0.387	20.5 / 0.077	39.0 / 0.931	32.0 / 0.489
	<i>Tellina</i> sp.	24.0 / 0.161	1.0 / < <b>0.001</b> *	18.0 / <b>0.050</b> *	19.0 / 0.063
	Nemertea spp.	30.0 / 0.387	19.0 / 0.063	23.0 / 0.136	22.0 / 0.113
	Nemertea sp. A	28.0 / 0.297	8.50 / <b>0.003</b> *	17.0 / <b>0.040</b> *	35.5 / 0.666
12 Oct. 1995	<i>Polygordius jouinae</i>	31.0 / 0.436	26.0 / 0.222	36.0 / 0.730	32.0 / 0.489
	<i>Syllides convoluta</i>	6.0 / < <b>0.001</b> *	13.5 / <b>0.014</b> *	40.0 / 1.00	29.0 / 0.340
	<i>Caulleriella</i> sp.	32.0 / 0.489	38.5 / 0.863	40.0 / 1.00	32.0 / 0.489
	<i>Spisula solidissima</i>	28.0 / 0.297	21.5 / 0.094	33.0 / 0.546	36.0 / 0.730
	<i>Peosidrilus</i> spp.	13.5 / <b>0.014</b> *	9.0 / <b>0.004</b> *	40.5 / 1.00	35.5 / 0.666

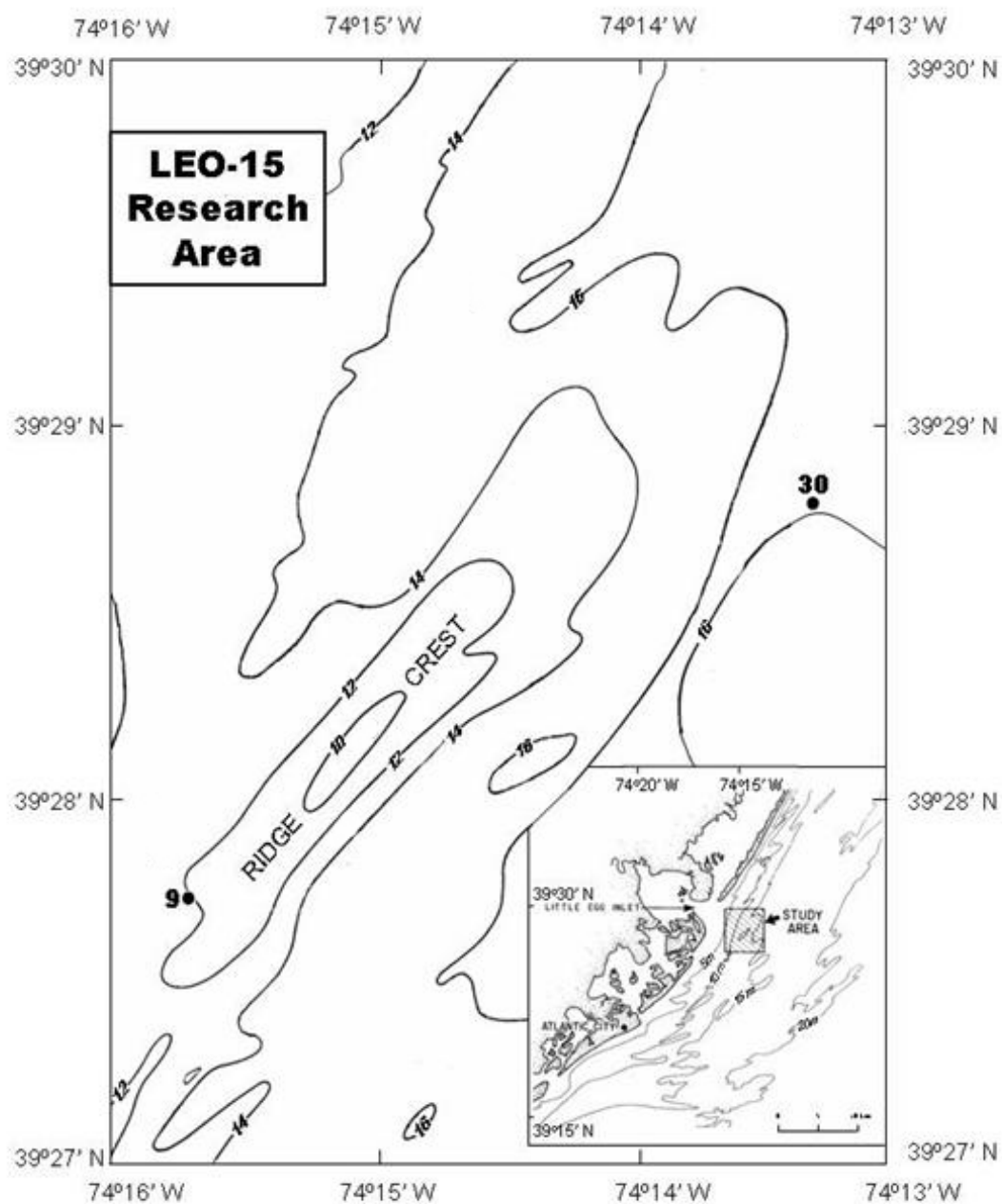


Fig. 2.1. Bathymetry of Beach Haven Ridge at LEO-15 showing sampling Sta. 9 on the inshore side of the ridge and Sta. 30 offshore of the ridge (modified from Weissberger and Grassle 2003)

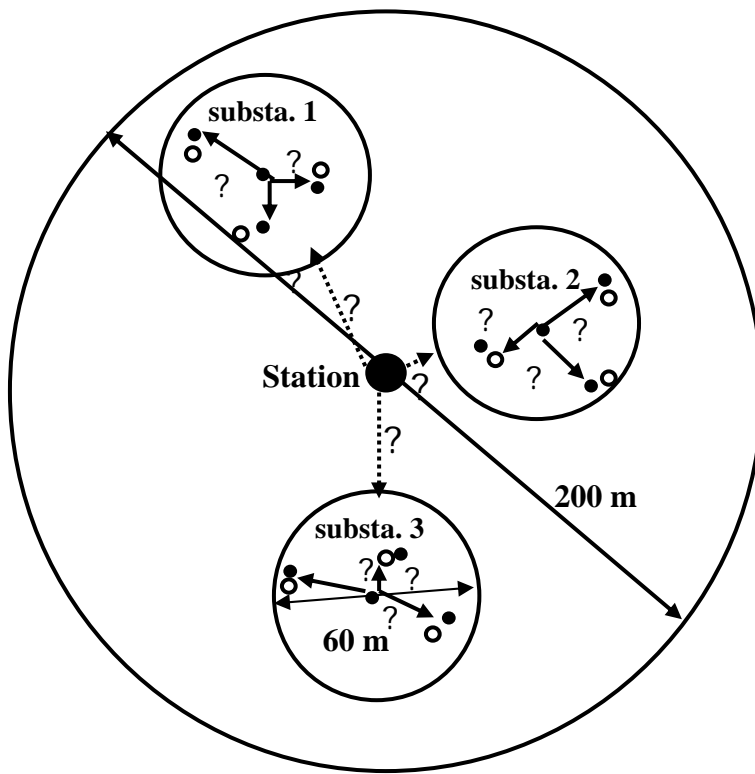


Fig. 2.2. Partially randomized, nested sampling design for Sta. 9 and Sta. 30 at LEO-15. Triplicate paired crest and trough samples  $<1$  m apart were nested within three 60-m diameter circles (substations), nested within a 200-m diameter circle at each station (9 and 30). The stations are  $\sim 4$  km apart. Station denotes permanent station mooring, filled circle in center of substation indicates permanent substation mooring, question marks (?) denote random distances and circles are paired crest (i.e., open) and trough (i.e., filled) samples ( $n=6$  cores substation<sup>-1</sup> [3 crests, 3 troughs]; 18 cores station<sup>-1</sup>) on each sampling date.

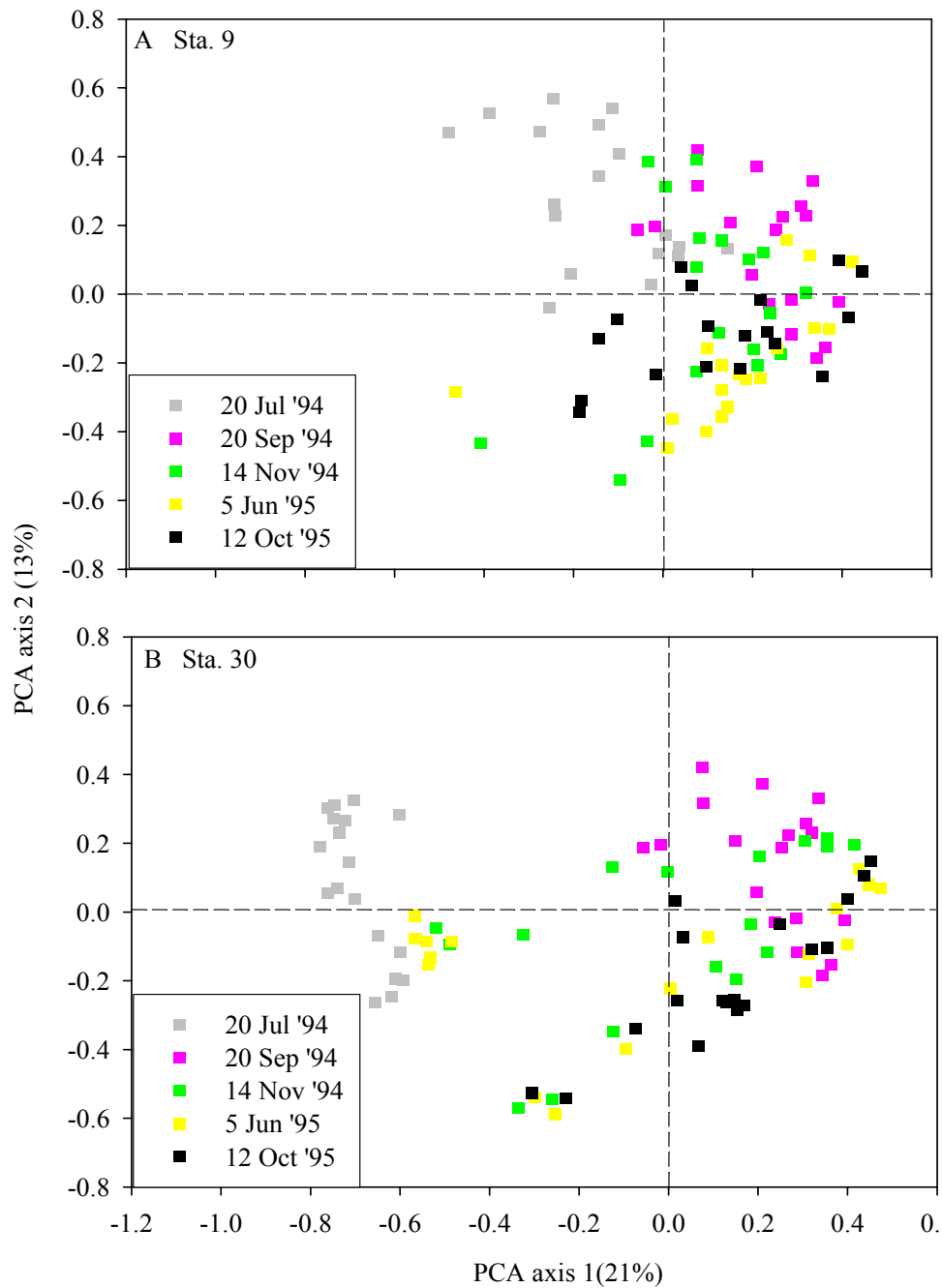


Fig. 2.3. PCA-H metric scaling ordination of macrofaunal core assemblage spatial patterns based on CNESS ( $n = 10$  individuals) for (A) Sta. 9 and (B) Sta. 30. The first two axes explain 21 and 13 % of the variance respectively. Core samples taken on

different dates are indicated by different colors with 20 July 1994= grey, 20 September 1994=pink, 14 November 1994=green, 5 June 1995=yellow and 12 October 1995=black.

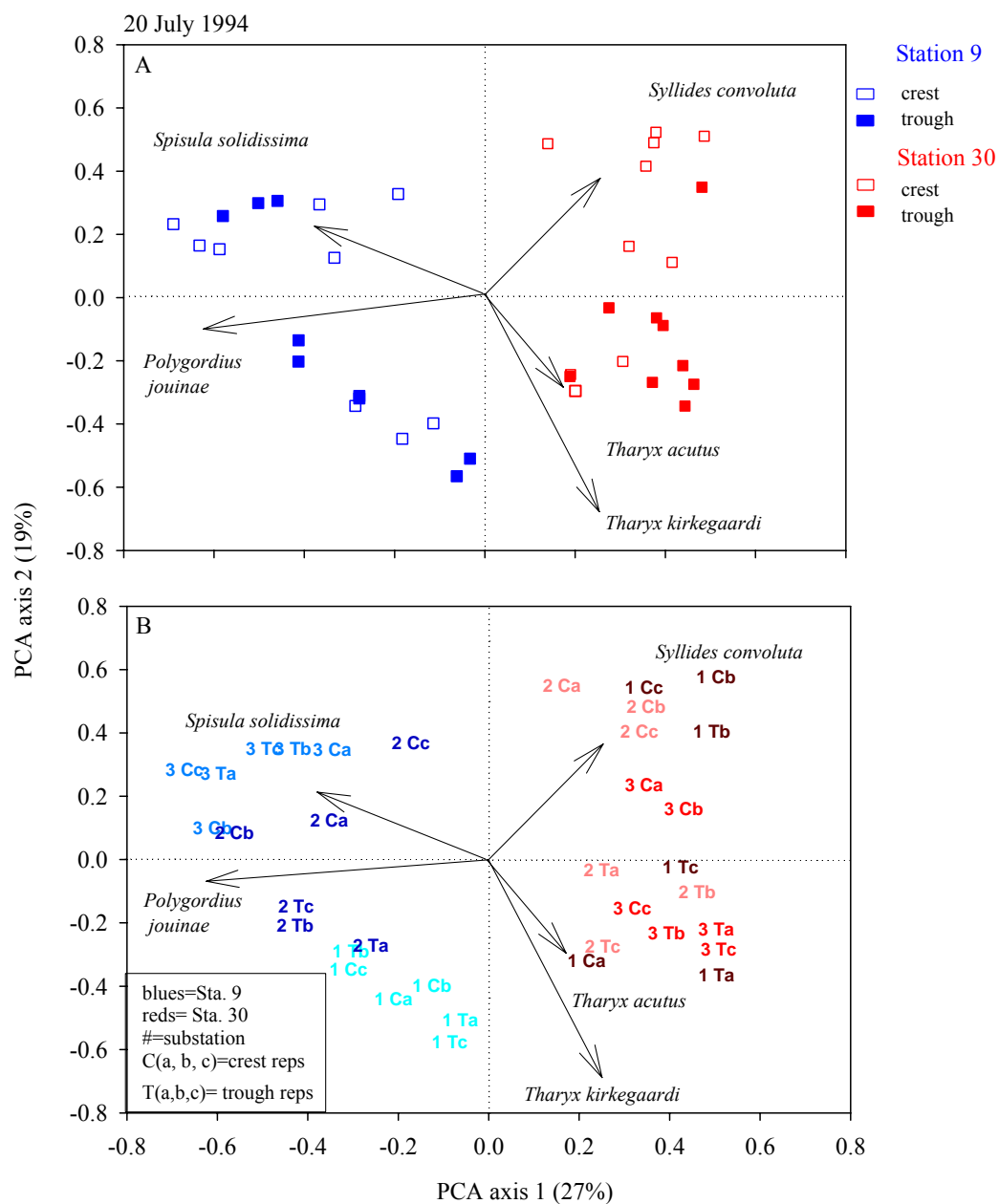


Fig. 2.4. PCA-H metric scaling ordination of macrofauna core assemblage spatial patterns for 20 July 1994 sampling date at Sta. 9 and 30 based on CNESS ( $n = 10$  individuals). The first two axes explain 28 and 18 % of the variance respectively. Species vectors (Gabriel Euclidean distance biplot) have been overlaid on community ordination to show which species contribute to CNESS variation among samples and therefore drive spatial

patterns. Individual cores represented in (A) with squares, labeled according to station and habitat from which they were collected with Sta. 9 =blue, Sta. 30=red, crests=open squares and troughs=shaded squares, (B) with a series of colored numbers and letters according to station with Sta. 9=shades of blue, Sta. 30 shades of red, substations= 1-3 (spatial scale  $\leq 200$  m), habitat (crest =C, trough=T: spatial scale  $< 1$  m) and sampling point=a-c (spatial scale  $\leq 60$  m).



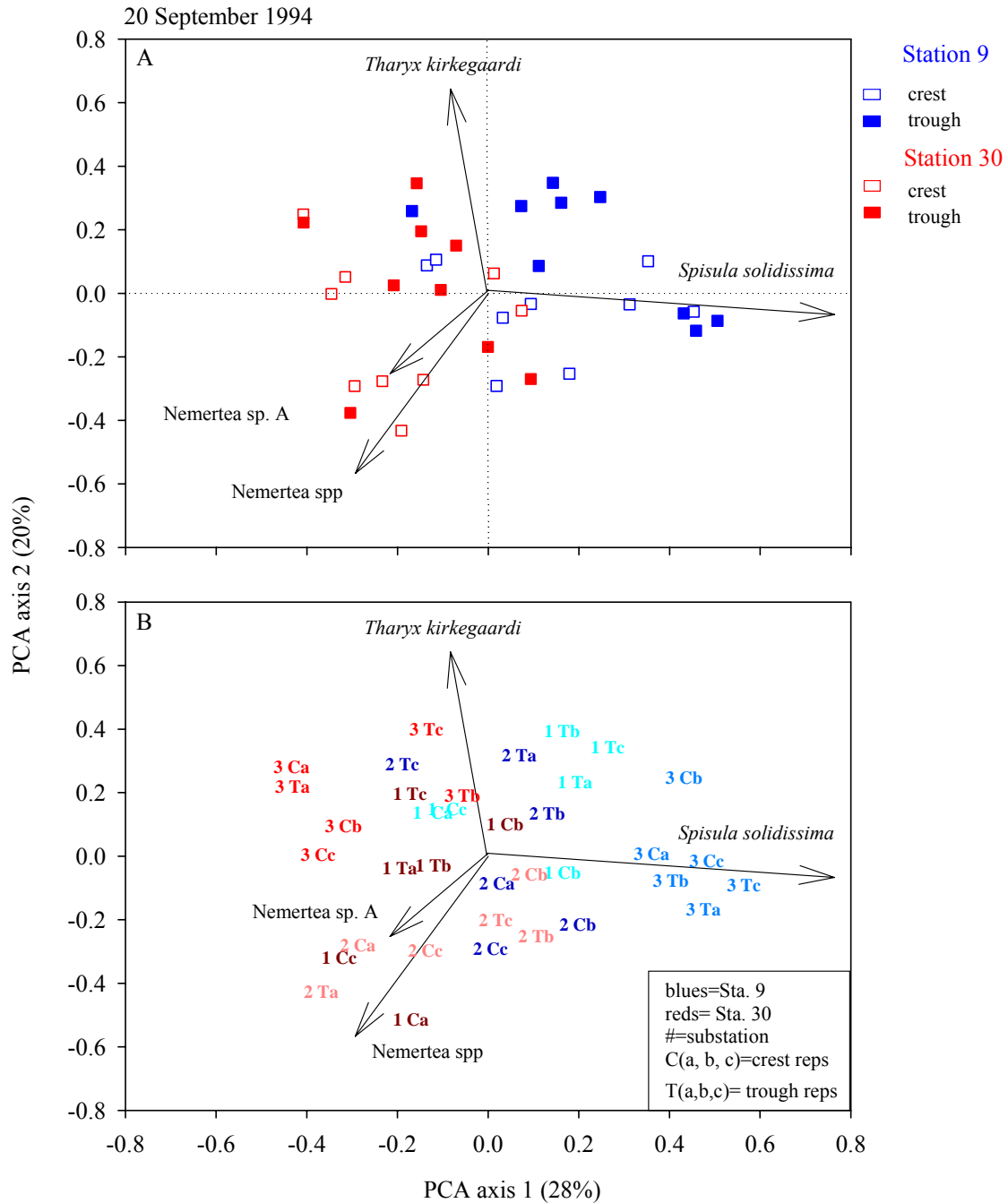


Fig. 2.5. PCA-H metric scaling ordination of macrofauna core assemblage spatial patterns for 20 September 1994 sampling date at Sta. 9 and 30 based on CNESS ( $n = 10$  individuals). The first two axes explain 28 and 20 % of the variance respectively. Species vectors (Gabriel Euclidean distance biplot) have been overlaid on community ordination

to show which species contribute to CNESS variation among samples and therefore drive spatial patterns. Individual cores represented in (A) with squares, labeled according to station and habitat from which they were collected with Sta. 9 =blue, Sta. 30=red, crests=open squares and troughs=shaded squares, (B) with a series of colored numbers and letters according to station with Sta. 9=shades of blue, Sta. 30 shades of red, substations= 1-3 (spatial scale  $\leq 200$  m), habitat (crest =C, trough=T: spatial scale  $< 1$  m) and sampling point=a-c (spatial scale  $\leq 60$  m).

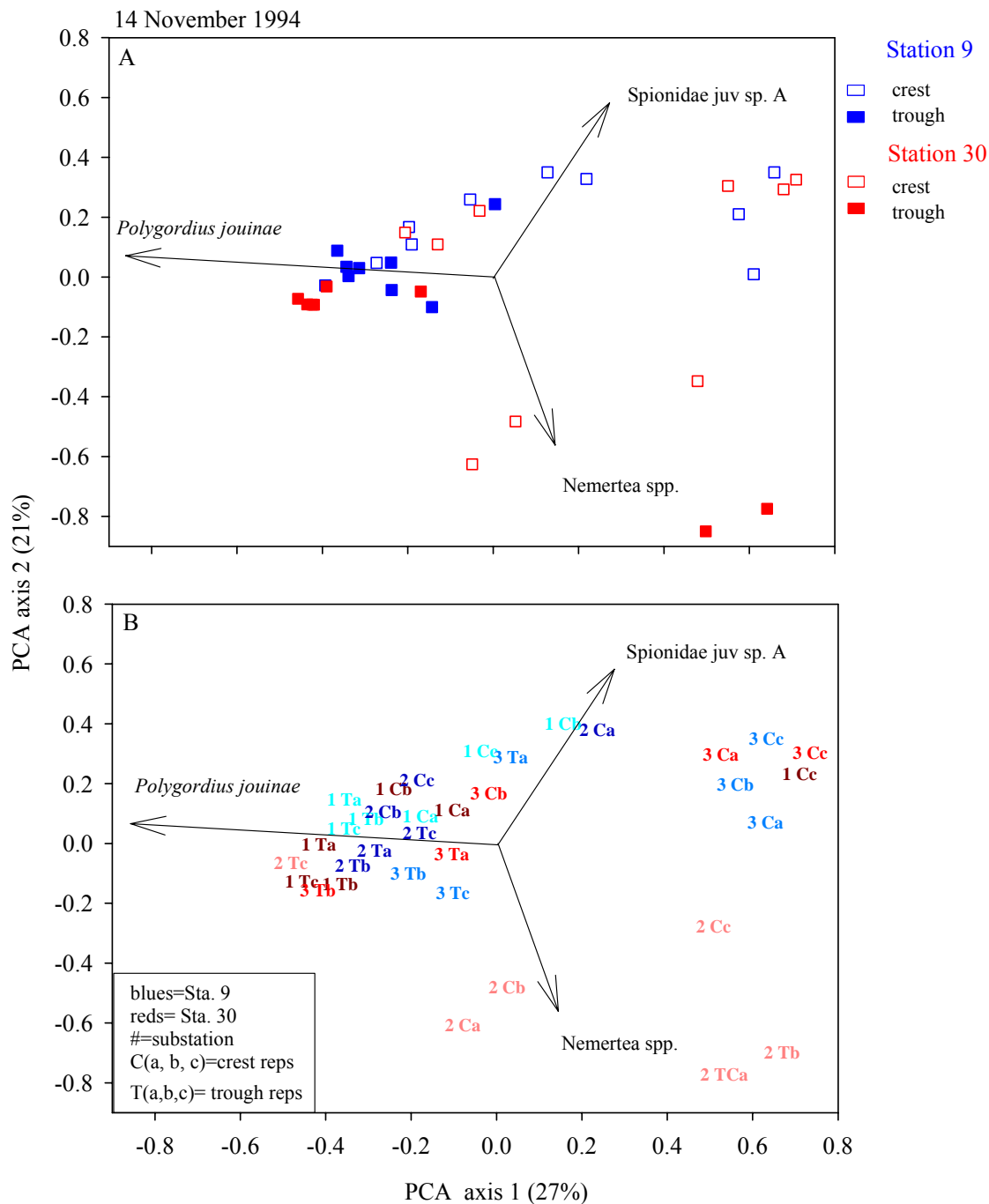


Fig. 2.6. PCA-H metric scaling ordination of macrofauna core assemblage spatial patterns for 14 November 1994 sampling date at Sta. 9 and 30 based on CNESS ( $n = 10$  individuals). The first two axes explain 27 and 21 % of the variance respectively. Species vectors (Gabriel Euclidean distance biplot) have been overlaid on community ordination

to show which species contribute to CNESS variation among samples and therefore drive spatial patterns. Individual cores represented in (A) with squares, labeled according to station and habitat from which they were collected with Sta. 9 =blue, Sta. 30=red, crests=open squares and troughs=shaded squares, (B) with a series of colored numbers and letters according to station with Sta. 9=shades of blue, Sta. 30 shades of red, substations= 1-3 (spatial scale  $\leq 200$  m), habitat (crest =C, trough=T: spatial scale  $< 1$  m) and sampling point=a-c (spatial scale  $\leq 60$  m).

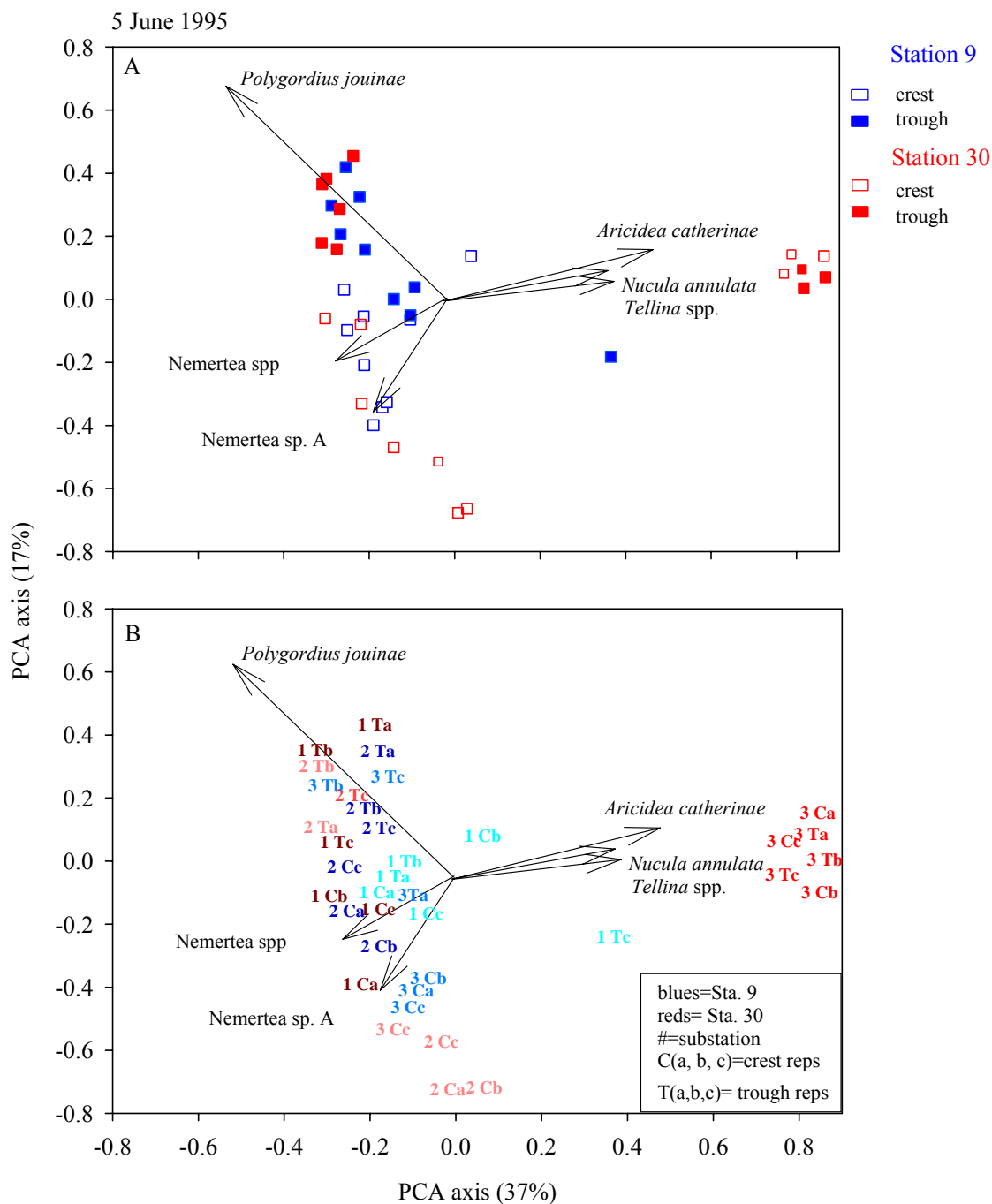


Fig. 2.7. PCA-H metric scaling ordination of macrofauna core assemblage spatial patterns for 5 June 1995 sampling date at Sta. 9 and 30 based on CNESS ( $n = 10$  individuals). The first two axes explain 37 and 17 % of the variance respectively. Species vectors (Gabriel Euclidean distance biplot) have been overlaid on community ordination to show

which species contribute to CNESS variation among samples and therefore drive spatial patterns. Individual cores represented in (A) with squares, labeled according to station and habitat from which they were collected with Sta. 9 =blue, Sta. 30=red, crests=open squares and troughs=shaded squares, (B) with a series of colored numbers and letters according to station with Sta. 9=shades of blue, Sta. 30 shades of red, substations= 1-3 (spatial scale  $\leq 200$  m), habitat (crest =C, trough=T: spatial scale  $< 1$  m) and sampling point=a-c (spatial scale  $\leq 60$  m).

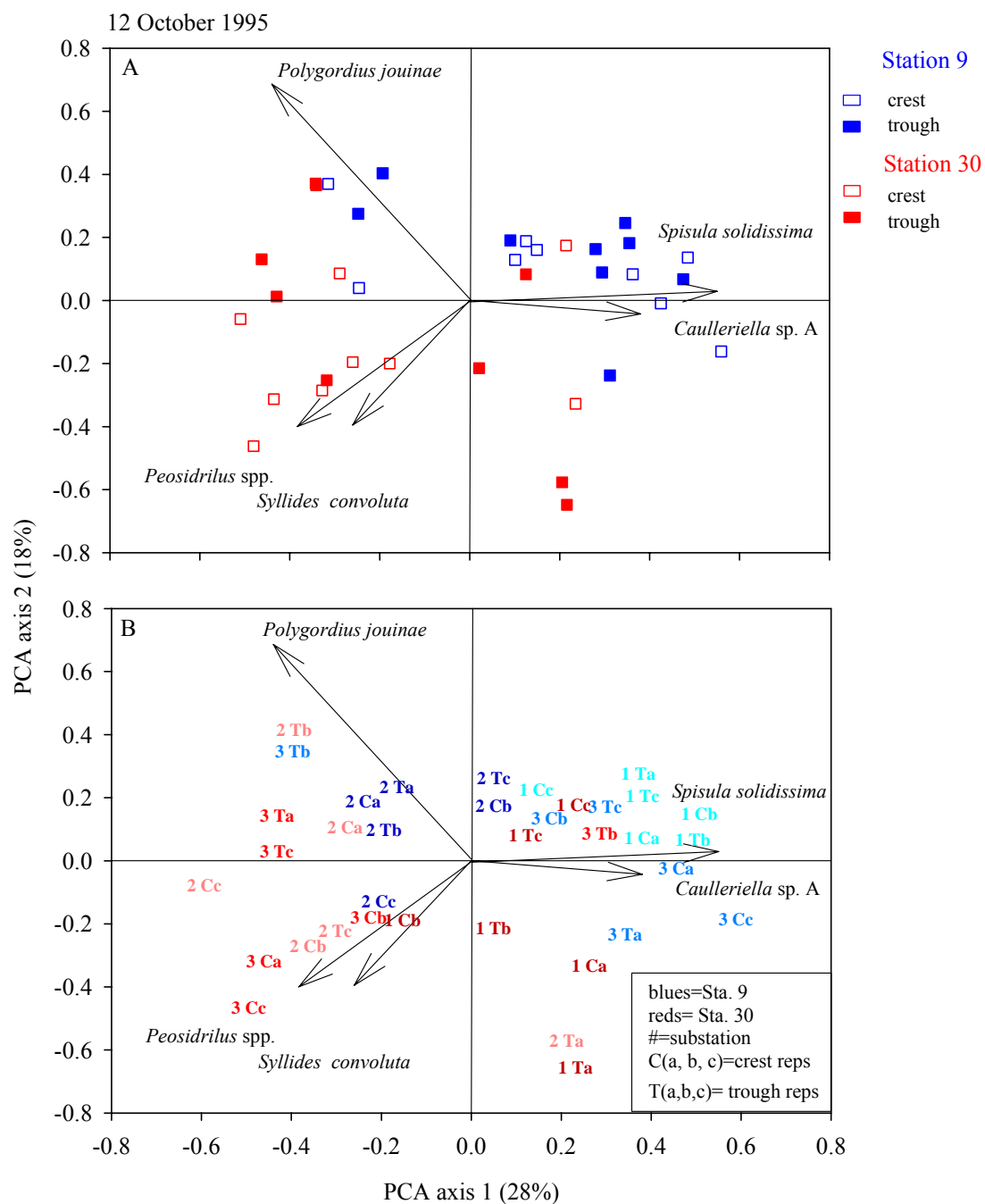


Fig. 2.8. PCA-H metric scaling ordination of macrofauna core assemblage spatial patterns for 12 October 1995 sampling date at Sta. 9 and 30 based on CNESS ( $n = 10$  individuals). The first two axes explain 28 and 18 % of the variance respectively. Species vectors

(Gabriel Euclidean distance biplot) have been overlaid on community ordination to show which species contribute to CNESS variation among samples and therefore drive spatial patterns. Individual cores represented in (A) with squares, labeled according to station and habitat from which they were collected with Sta. 9 =blue, Sta. 30=red, crests=open squares and troughs=shaded squares, (B) with a series of colored numbers and letters according to station with Sta. 9=shades of blue, Sta. 30 shades of red, substations= 1-3 (spatial scale  $\leq 200$  m), habitat (crest =C, trough=T: spatial scale  $< 1$  m) and sampling point=a-c (spatial scale  $\leq 60$  m).



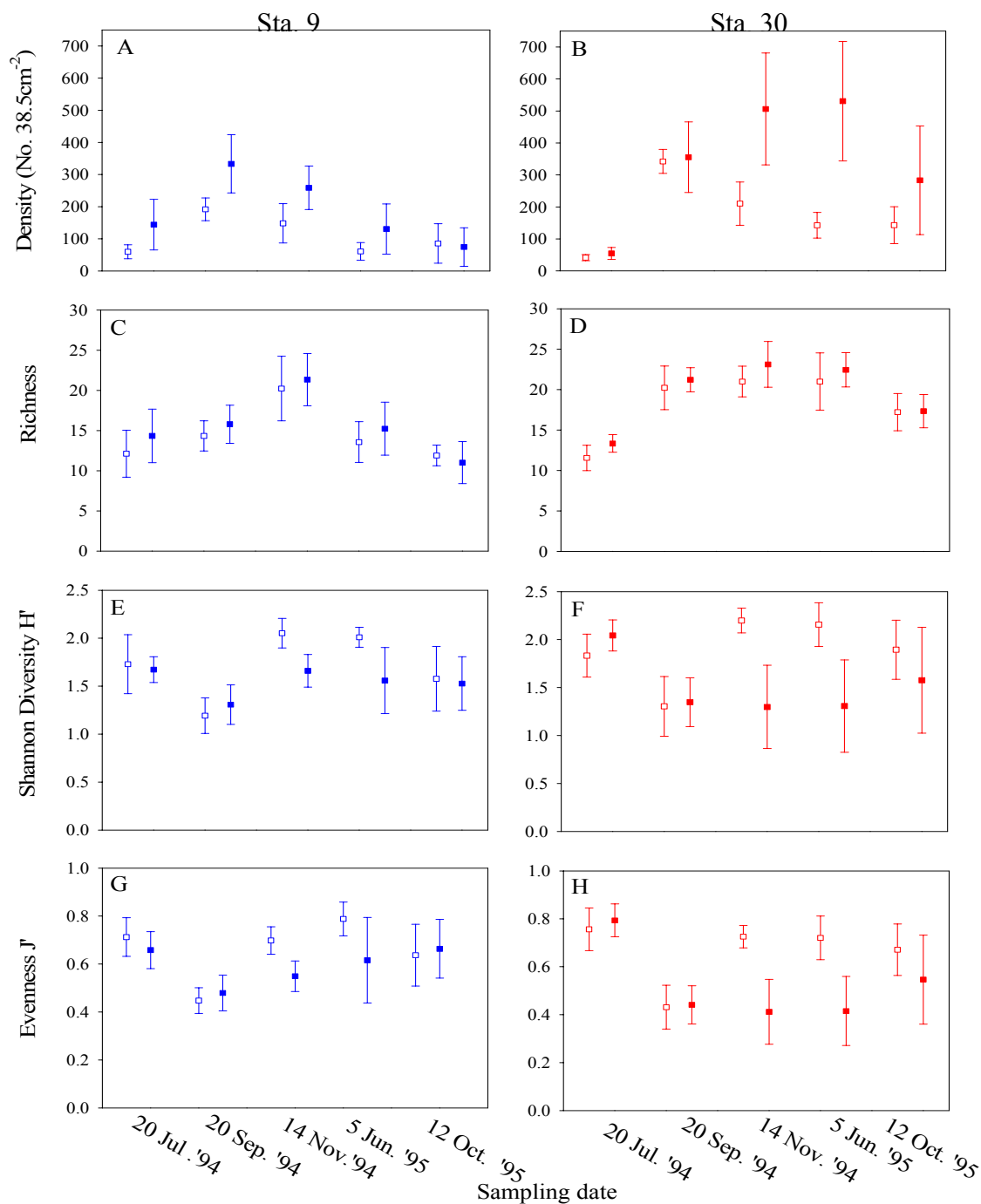


Fig. 2.9. Means ± 95% confidence intervals for (A, B) total density of macrofauna in ripple crests compared to troughs on each sampling date (20 July 1994, 20 September 1994, 14 November 1994, 5 June 1995 and 12 October 1995;  $n=90$ ) at station 9 and 30 respectively, (C, D) taxon richness, (E, F) Shannon diversity H', and (G, H) taxonomic

evenness  $J'$ . Crests=open squares and troughs=filled squares. Note scale on y-axes differs among panels.

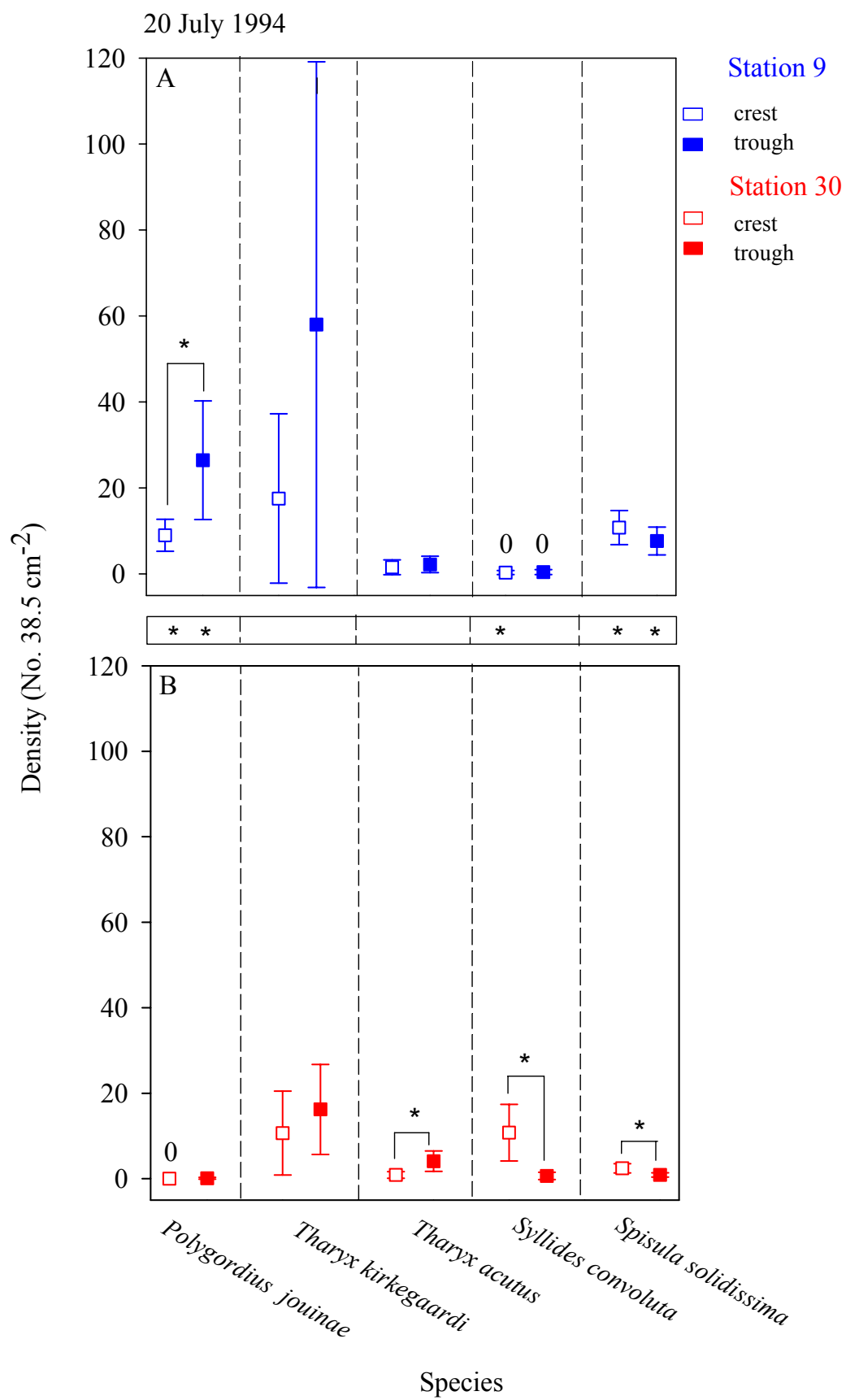


Fig. 2.10. Mean densities  $\pm$  95 % confidence intervals of taxa contributing to >5 % of CNESS variation in Gabriel biplots for samples taken 20 July 1994 from ripple crests and troughs at (A) Sta. 9, (B) Sta. 30. \* within station indicate significant differences between crests and troughs, and \* between plots A and B indicate significant differences in crests or troughs at Sta. 9 compared to Sta. 30.

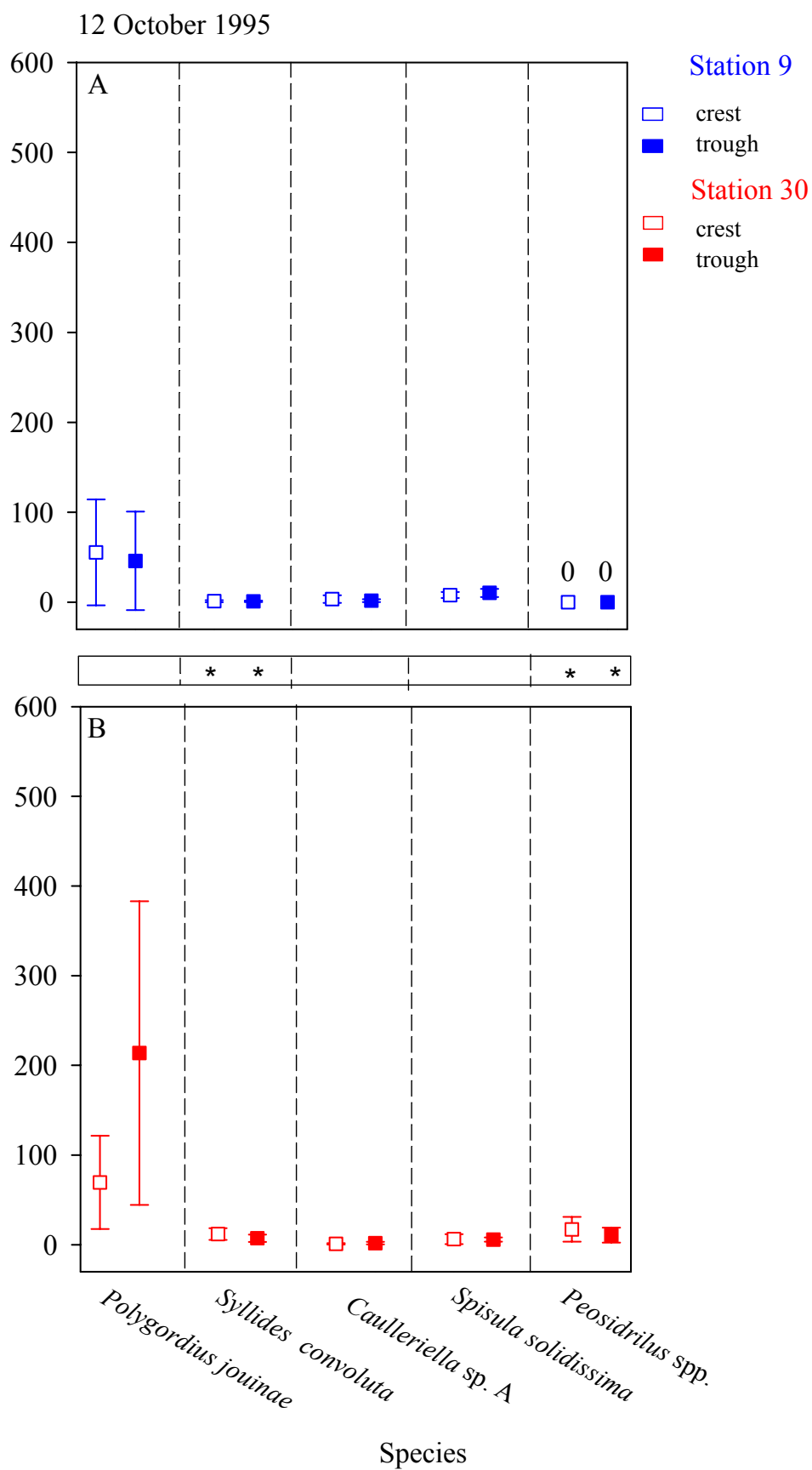


Fig. 2.11. Mean densities  $\pm$  95 % confidence intervals of taxa contributing to >5 % of CNESS variation in Gabriel biplots for samples taken 12 October 1995 from ripple crests and troughs at (A) Sta. 9, (B) Sta. 30. \* within station indicate significant differences between crests and troughs, and \* between plots A and B indicate significant differences in crests or troughs at Sta. 9 compared to Sta. 30.

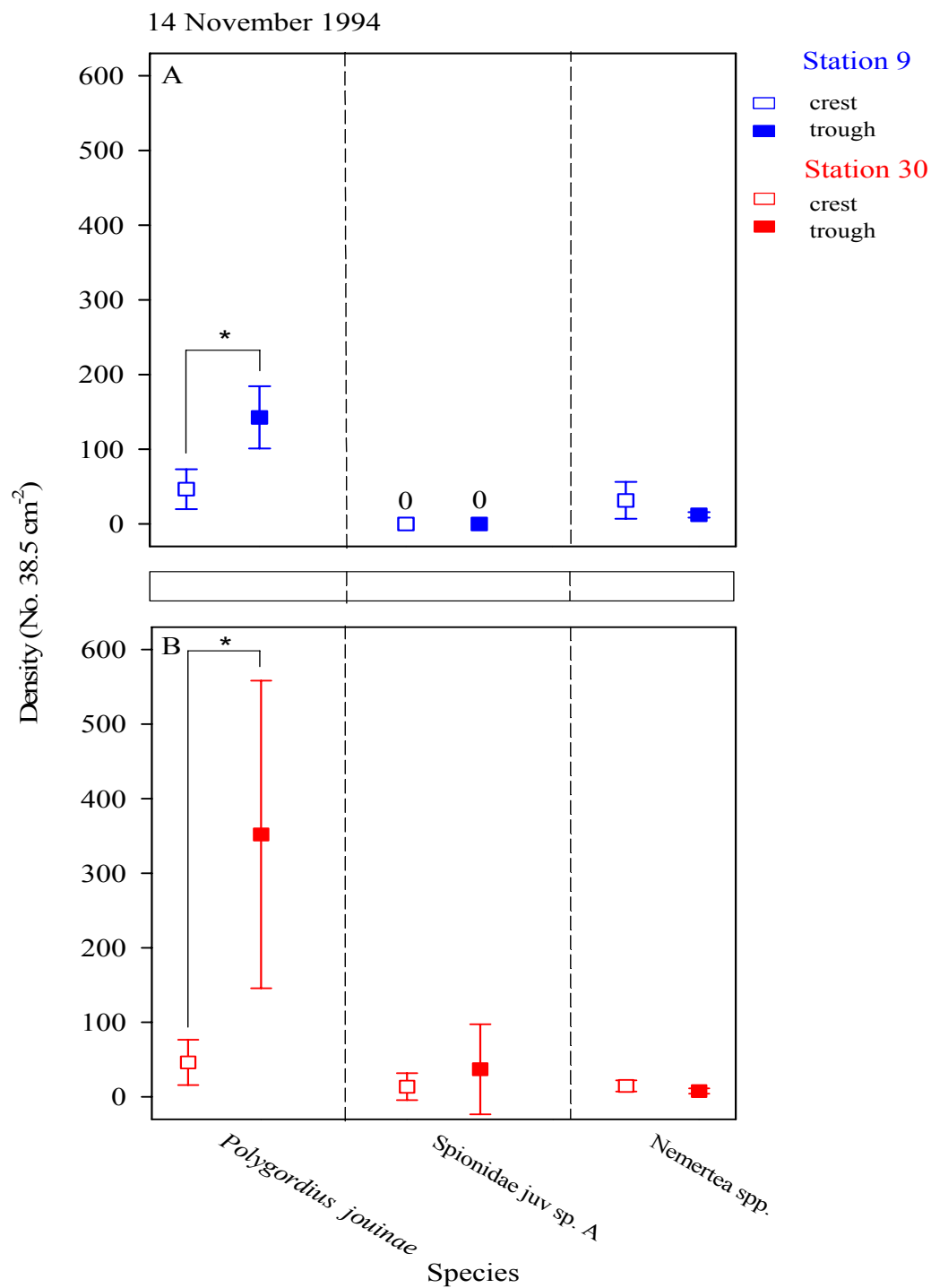


Fig. 2.12. Mean densities  $\pm$  95 % confidence intervals of taxa contributing to >5 % of CNESS variation in Gabriel biplots for samples taken 14 November 1994 from ripple crests and troughs at (A) Sta. 9, (B) Sta. 30. \* within station indicate significant

differences between crests and troughs, and \* between plots A and B indicate significant differences in crests or troughs at Sta. 9 compared to Sta. 30.



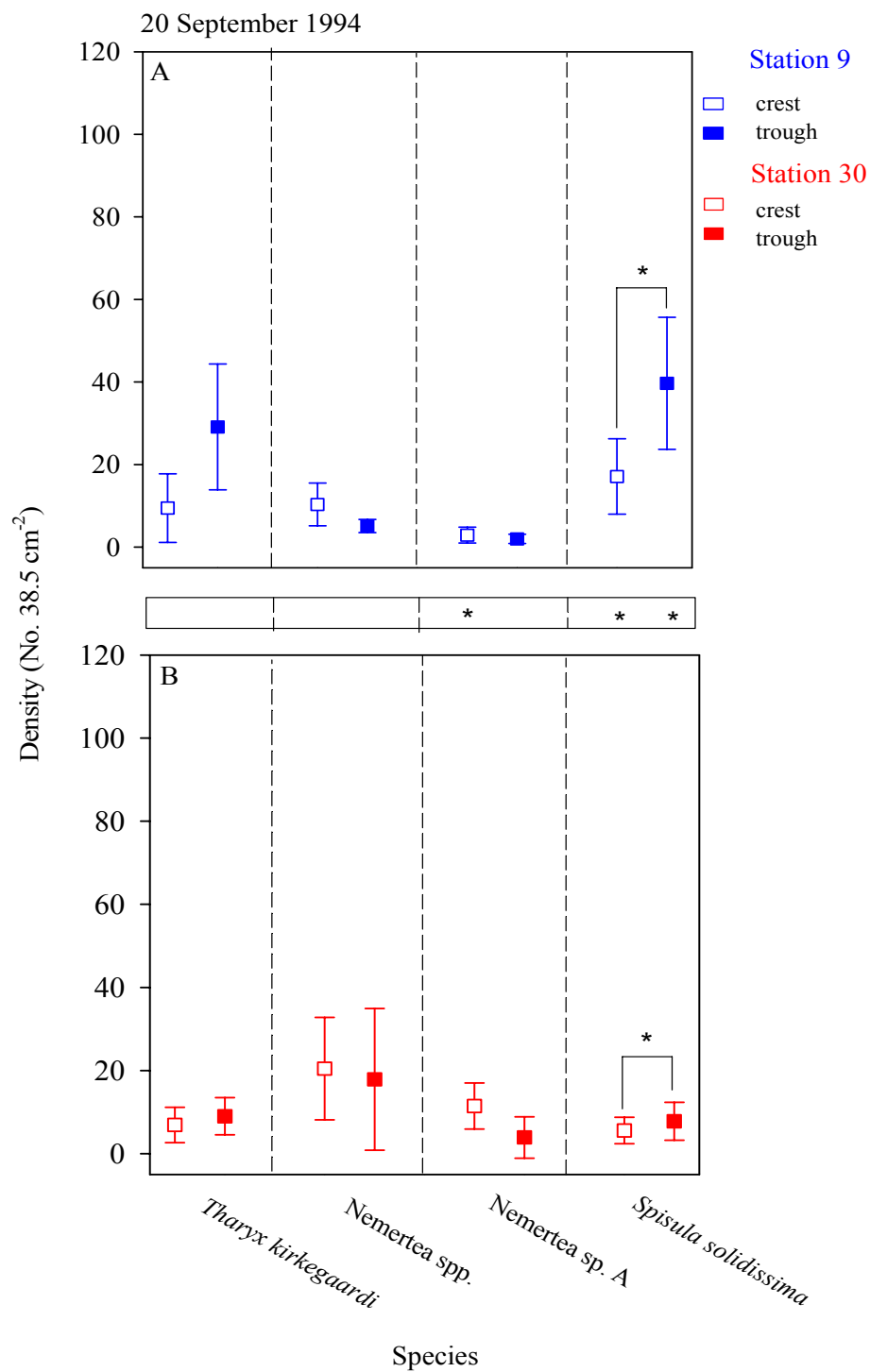


Fig. 2.13. Mean densities  $\pm$  95 % confidence intervals of taxa contributing to >5 % of CNESS variation in Gabriel biplots for samples taken 20 September 1994 from ripple

crests and troughs at (A) Sta. 9, (B) Sta. 30. \* within station indicate significant differences between crests and troughs, and \* between plots A and B indicate significant differences in crests or troughs at Sta. 9 compared to Sta. 30.

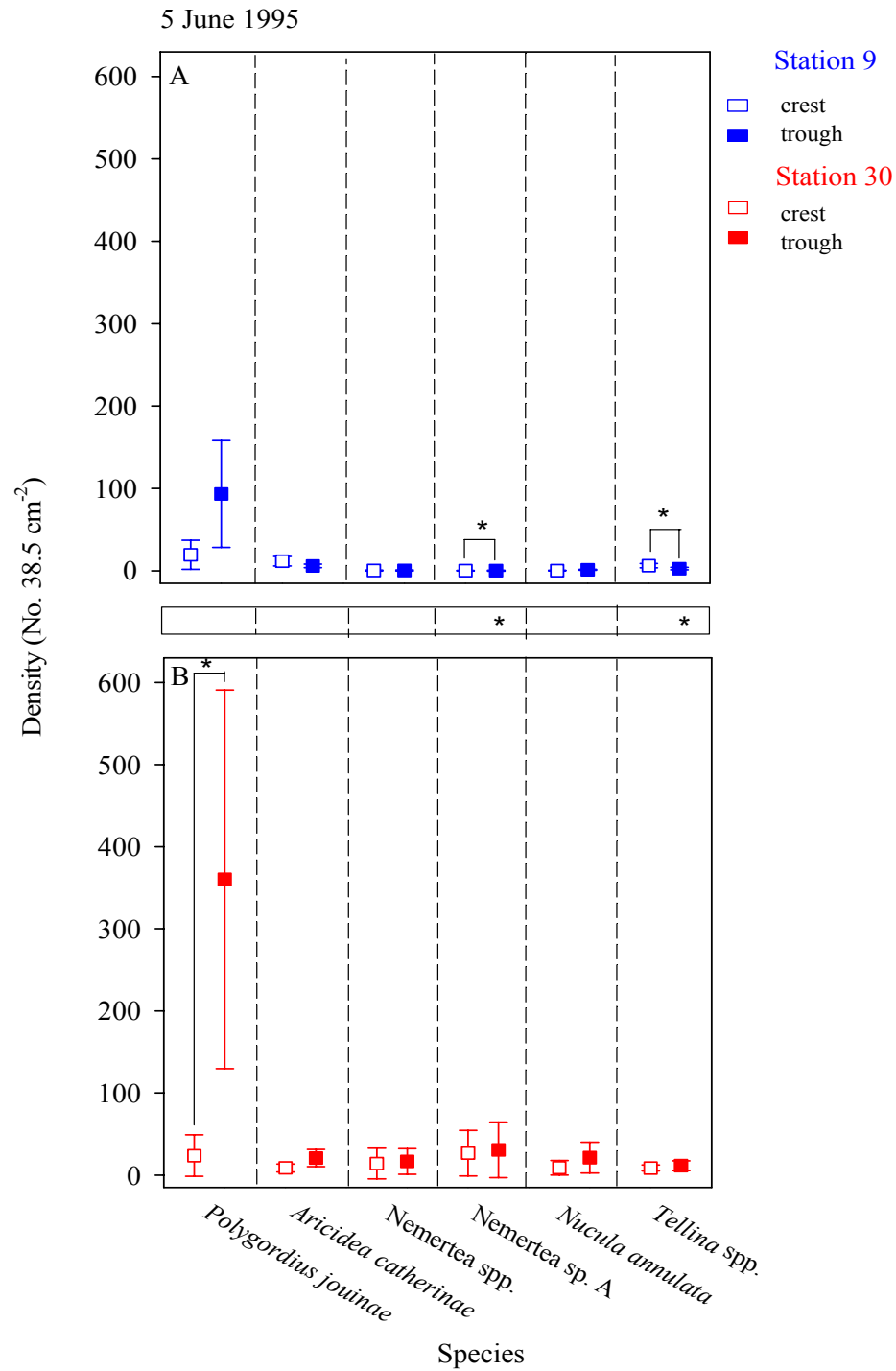


Fig. 2.14. Mean densities  $\pm$  95 % confidence intervals of taxa contributing to >5 % of CNESS variation in Gabriel biplots for samples taken 5 June 1995 from ripple crests and

troughs at (A) Sta. 9, (B) Sta. 30. \* within station indicate significant differences between crests and troughs, and \* between plots A and B indicate significant differences in crests or troughs at Sta. 9 compared to Sta. 30.

**CHAPTER 3**  
**ECOLOGICAL HETEROGENEITY: SMALL-SCALE, PATCHY**  
**DISTRIBUTIONS OF MACROFAUNAL SPECIES IN AN ECOLOGICAL**  
**CONTEXT**

**INTRODUCTION**

One of the most basic ways of characterizing a community is by habitat type and the first step in examining population and community patterns is to define and determine the number and spatial arrangement of habitats in the area of interest prior to taking biological samples. The role of habitat in influencing the structure and dynamics of populations and communities has been emphasized for both terrestrial and marine environments (e.g., Able et al. 2003; Diaz et al. 2003; Morris 2003; Zajac et al. 2003). Availability, quality, size, and spacing of habitat patches have direct effects on populations or communities by providing suitable living conditions (often species specific) in some areas but not others (Chapman 1994; Underwood et al. 2000). Indirect effects include interactions among individuals or species (Menge et al. 1985; Fairweather 1988). It is well known that the scale of sampling, relative to the distributional pattern of organisms to be sampled, can influence both the precision and interpretation of data (Thrush et al. 1994). However, a top down approach where population and community patterns are studied within the context of defined habitats occurring at repeated intervals in space, has been more commonly employed in terrestrial and intertidal landscapes where species distributions and habitats are readily visible (e.g., Underwood and Chapman 1996; Kent et al. 1997). Due to logistical constraints, research on subtidal

macrofaunal communities has more often focused on scale-dependent factors without adequately defining or quantifying habitat(s) over time or space.

Most commonly, spatial distributions and composition of subtidal habitats and macrofaunal communities have been interpolated from point samples randomly collected via remote or “blind” bottom grabs with little explicit a priori consideration given to habitat type (e.g., topographic features) or spatial arrangement of habitats beyond sediment distributions (Zajac et al. 2003). An outstanding feature of soft-sediment macrofaunal communities is that both abundances and species composition vary greatly at a variety of spatial scales (cm to km), and patchy distributions are very common at small scales (cm to m). Such patchiness can confuse interpretation of community pattern, especially if patterns are documented with samples collected at scales larger than those relevant to the infauna. Hall et al. (1994) observed that samples from subtidal, soft-sediments are not generally taken with sufficient spatial resolution to examine small-scale differences in community structure.

A host of abiotic and biotic factors create and maintain macrofaunal population and community structure at a variety of spatial scales (reviewed by Ólafsson et al. 1994; Snelgrove and Butman 1994) and the ecological patterns and processes operating at one spatial scale may differ from those at another scale (Dayton and Oliver 1980; Levin and Huggett 1990; Whitlatch et al. 1998). It has been suggested that patchiness (Whitlatch 1980), along with a lack of appropriate spatial replication of samples (Hurlbert 1984), make it difficult to elucidate which factor (s) are most important in influencing macrofaunal community structure. Nested sampling designs have been recommended as a way to characterize the large variation within marine soft-sediment communities, and to

aid in understanding how community patterns are formed (Morrisey et al. 1992; Ramey and Snelgrove 2003). More recently, advances in imaging techniques have shown subtidal, soft-sediment landscapes to be heterogeneous and complex, containing a rich array of habitats or patch structures (e.g., Able et al. 2003; Diaz et al. 2003; Zajac et al. 2003) that appear to be significant for benthic organisms. Side-scan images of benthic landscapes in Long Island Sound identified six distinct large-scale (> km) habitats defined by sediment grain size (Zajac et al. 2003). Within these, further habitat heterogeneity was present at spatial scales of kilometers to meters, and even smaller scales of < 1 m defined by distinct sediment patches, and biogenic structures (e.g., pits, mounds, and burrows) (Zajac et al. 2003). At scales ranging from square meters to kilometers, infaunal populations exhibited complex and spatially varying patterns of abundance in relation to habitat. Chapter 2 of this dissertation showed that in hydrodynamically disturbed sandy sediments on the continental shelf, habitats and distinct communities persisted over time and space. Several individual taxa showed significantly greater densities in either crests or troughs of sand ripples. Thus, a priori knowledge of whether a benthic sample came from a crest or trough rather than taking “blind” random samples helped to explain some of the small-scale macrofaunal patchiness often observed in relatively homogeneous, well sorted sandy sediments. Analysis of pattern in relation to habitat may help identify the scales over which particular processes and mechanisms are important and aid in the design of experimental studies.

A key question in the present study was whether community patterns at relatively small scales (i.e., cm to m) can be related to defined topographic features, and what

features of these habitats (e.g., sediment properties) create observed macrofaunal patterns. This research is a logical extension of the previous Chapter, focusing on habitats and community patterns within the smallest scale examined (i.e., 60 m). Camera and video images were used to define and characterize habitats that were frequently encountered at small scales of <1 m along a 44-m transect including ripple crests, flanks, troughs with shell hash in them, and troughs without shell hash. Moreover, a suite of sediment properties including grain size and food quality measures (e.g., chl *a*, phaeophytin, particulate organic carbon, and nitrogen) were examined simultaneously with macrofaunal samples to aid in understanding observed macrofaunal patterns and to generate hypotheses for experimental studies in subsequent Chapters.

## MATERIALS AND METHODS

### Sampling design

In July and August 2004, a SCUBA diver-operated, handheld video camera was used to film the benthic environment at Sta. 9 (Fig.1.1) to define and characterize the habitats present within 1-m<sup>2</sup> plots. Five habitats were frequently found within these plots: ripple crests, flanks, troughs with shell hash (trough +SH), troughs without shell hash (troughs –SH), and tubes made by the polychaete *Diopatra cuprea*. On 9 June, 2005 a 44-m transect was set up at Sta. 9 (i.e., the transect was perpendicular to the ripples and prevailing current). Four macrofaunal core samples were collected from each of 12, 1-m<sup>2</sup> quadrats on either the left or right side (determined randomly) of the transect using a hand held corer (7-cm diameter, 10 cm deep, 38.5 cm<sup>2</sup>) (Fig. 3.1). The four macrofaunal cores were collected from four of the five habitats characterized in 2004 (1 core habitat<sup>-1</sup>=



4 cores quadrat<sup>-1</sup>,  $n=48$ ). Habitats sampled included ripple crests, flanks, troughs +SH, and troughs -SH (Fig. 3.1). Initially I wanted to include the habitat immediately surrounding *D. cuprea* tubes but few tubes were present at Sta. 9 in June 2005. Along the transect a nested, hierarchical sampling design was set up where each of a series of successively smaller spatial scales were nested within larger scales (Fig. 3.1). Spatial scales of interest included <1-m, 2-m and 4-m. Separate sediment cores were collected for grain size and sediment analyses (i.e., carbon, nitrogen, chl *a* and phaeophytin) using weighted, modified syringe cores (5.3 cm<sup>2</sup> and 8 cm long). Sediment cores were taken as close as possible to each macrofaunal core (2 syringe cores habitat<sup>-1</sup> = 8 syringe cores quadrat<sup>-1</sup>,  $n=96$ ).

Macrofaunal core samples were sieved over a 300- $\mu$ m mesh screen, fixed in 10% formalin and seawater mixture, and then promptly transferred to 70% ethanol with rose bengal. Macrofauna were identified to the lowest taxonomic level possible (i.e., genus or species). In some cases, small juveniles could not be identified and were grouped by Family or some higher level of classification and referred to as spp. Sediment grain size analysis was conducted using stacked sieves ( $\geq 2$  mm, 1 mm, 500  $\mu$ m, 250  $\mu$ m, 125  $\mu$ m, 32  $\mu$ m,  $\leq 32$   $\mu$ m). For analytical purposes sediments were described as medium to coarser grained ( $\geq 250$   $\mu$ m) or finer grained ( $<250$   $\mu$ m). A small amount of sediment was removed from the top layer ( $\sim 1$  cm deep) of syringe cores taken for sediment analysis and frozen for later determination of ambient concentrations of total carbon, nitrogen, chlorophyll-*a*, and phaeopigment. Sediment for carbon and nitrogen analysis was first dried, ground, and acidified in silver cups to remove carbonates and then measured using a Fisons NA1500N elemental analyzer with acetanilide as a calibration standard. Combined chl *a*

and phaeopigment was extracted from sediment (3-11 g) in 90% acetone and determined by fluorometric analysis on a Hitachi F2000 spectrofluorometer (modified from Strickland and Parsons 1972; APHA 1992).

### Data Analysis

Community composition was compared among habitats and quadrats on individual macrofaunal cores using CNESS (Chord Distance Normalized Expected Species Shared) as described by Trueblood et al. (1994). CNESS is an extension of Orlóci's (1978) chord distance and Grassle and Smith's (1976) NESS (Normalized Expected Species Shared). This particular index was used because it is sensitive to rare as well as abundant species. Distribution patterns were clustered using weighted, pair-group mean average sorting of CNESS dissimilarities along with a metric scaling of CNESS using COMPAH 96 and Matlab programs written by Eugene D. Gallagher, University of Massachusetts, Boston.

The hypergeometric probability matrix (H) that was produced by metric scaling of CNESS was then analyzed by principal components (PCA-H). Species that contribute to CNESS variation among samples are displayed in a Gabriel Euclidean distance biplot overlay (Gabriel 1971; Ter Braak 1983), where the length and angle of species vectors indicate the contribution of the species to the PCA-H axes. Species that contributed >2% to CNESS variation were included in the biplots. Average densities of species shown to be influential in creating the spatial pattern from the biplots (those that contributed to >2% of CNESS variation) were compared among the four habitats by plotting means with 95% confidence intervals for each sampling date and station. Community measures

including density of total macrofauna, taxon richness, Shannon-Wiener diversity  $H'$  (base 2), and evenness  $J'$  were also compared in the same manner. To determine whether there were significant differences in any of these measures among the four habitats a non-parametric test (Mann-Whitney U) was performed in SPSS 10.0.

I evaluated variation in macrofaunal communities, both among habitats and among quadrats, with a nested AMOVA (Analysis of Molecular Variance), using GenAlEx 6.0 software (<http://www.anu.edu.au/BoZo/GenAlEx/>) (Peakall and Smouse 2006). AMOVA partitions the variation in community composition within and among quadrats, and within and among habitats based on both species composition and abundance, rather than on the abundance of any single species or some summary measure such as species richness or diversity, as could be done with ANOVA. Like molecular data, benthic data often deviate strongly from the assumption of being normally distributed, necessary for traditional ANOVA tests, and the data are inherently highly multivariate. With AMOVA, benthic data with multiple species and low abundances can easily be managed for non-parametric methods of evaluation. The analysis was originally designed for multiple genetic markers (here represented by multiple species/taxa), and individuals can easily be nested into “populations” (here represented by individual macrofaunal cores) and “regions” (here represented by the locations from which the cores were collected). Two different types of “regions”, namely habitats (i.e., ripple crest, flank, trough +SH and trough -SH) or quadrats (i.e., 1-12) were evaluated. For an individual core, each individual of a taxon was scored as 1 for that taxon and 0 for the others. For example, if a particular taxon had a total abundance of 7 in a single core, then there were 7 rows of the analysis that were ‘1’ for that taxon. GenAlEx first converts this

binary data set to a Euclidean distance matrix, and uses the elements of the matrix to calculate Sums of Squares (SS) as sums of squared distances. From this, Mean Squares (MS) and estimated variances were calculated within and among habitats as well as within and among quadrats. To determine whether the variance components were significant, a null-distribution was computed by re-sampling the data. For each permuted data set (99 iterations), each specimen was randomly allocated to a single core, keeping the total macrofaunal abundance for each core as it was originally. Thus, each specimen shows up once in each random data set, but the sampling structure is maintained as a constant. For each randomized data set, the resulting variance components were computed, as well as a variance ratio test criterion. The null hypothesis of random compositions in the data was then tested by comparing the actual test criterion with the null distribution of randomly produced test criteria, providing a non-parametric assessment of the probability of achieving at least as large a deviation from randomness as actually found for the data, by chance alone. The non-parametric test does not depend on normality of the data, and it allows one to test for homogeneity or heterogeneity of the entire community assemblage, rather than conducting a separate test for each of numerous taxa, or concentrating on a taxonomically less-informative feature such as species richness or species diversity.

Principal components analysis (PCA) was used to determine differences among the four habitats based on environmental variables, including sediment grain size (i.e. medium to coarser grained  $\geq 250 \mu\text{m}$  and finer sediments  $< 250 \mu\text{m}$ ) and indirect measures of food availability (i.e., total particulate organic carbon, chlorophyll-*a*, and phaeopigment) (SPSS 10.0). Values for nitrogen were not used in this analysis since they

were close to the detection limits of the elemental analyzer. Prior to analysis, variables were standardized to z-scores to weight all variables equally. To determine whether there were significant differences in environmental variables among the four habitats a non-parametric test (Mann-Whitney U) was performed in SPSS 10.0. Community measures and taxa contributing to >2% of CNESS variation in biplots were also linearly correlated with environmental variables.

## RESULTS

### Macrofaunal data

A total of 709 individuals were collected encompassing 35 different taxa. PCA-H analysis of macrofaunal cores indicated that core samples from the same habitat type clustered together (i.e., crests, flanks and troughs [+SH and -SH]) (Fig. 3.2A) rather than spatial arrangement along the transect (i.e., by quadrat) (Fig. 3.2B). Thus, samples collected close together (< 1 m apart) were more different from each other than samples taken further apart at distances of 2 to 44 m. Although three general habitat clusters were distinguishable, they were not well separated from each other in “PCA space”. The most distinct group was composed of samples collected from ripple crests (Fig. 3.2). Spatial arrangement along the transect was only evident for samples from crests and troughs (+SH and -SH) collected from quadrats 11 and 12 which tended to be more similar to each other than to the habitat that they were collected (Fig. 3.2B).

AMOVA results on community taxon composition and abundance data showed that the largest portion of the total variation (90%) occurred within individual cores, with the remaining 10% among cores (Table 3.1 A). Separate nested AMOVA's partitioned

the variance among and within-habitats as well as among and within-quadrats which accounted for 4% and 7%, and 2% and 8% of the total variance respectively (Table 3.1 B, C). The estimated variance component among habitats was almost twice as great as that among quadrats. Variance components were all significantly different from their null distribution averages (indicating departures from randomness). Within-habitat and within-quadrat variation were relatively similar to each other (i.e., variance fractions of 7 and 8 % respectively). This is reasonable considering the sampling design. For example, within-habitat variability also contained a spatial component (i.e., habitats sampled at different distances along a 44-m transect) and within-quadrat variability also contained a habitat component (i.e., 4 habitats sampled in each quadrat along the transect). Thus, within-habitat and within-quadrat components measured essentially the same variability. Given the above variance fractions an interaction among habitat and some spatial component of the sampling design also existed.

Comparisons of community measures among habitats indicated that total macrofaunal density, taxon richness, and diversity were greatest in ripple troughs -SH compared with the other three habitats. Macrofaunal density was only significantly greater in troughs -SH ( $\bar{x}=19.4$  ind.  $38.5 \text{ cm}^{-2}$ ) compared to ripple flanks where density was lowest ( $\bar{x}=10.4$  ind.  $38.5 \text{ cm}^{-2}$ ) (Fig. 3.3A; Table 3.2). Taxon richness and diversity were only significantly greater in troughs -SH (richness:  $\bar{x}=7.2$ ; diversity:  $\bar{x}=1.5$ ) compared to ripple crests (richness:  $\bar{x}=4.8$ ; diversity:  $\bar{x}=1.2$ ), (Fig. 3.3B, C; Table 3.2). Evenness values were significantly higher in flanks than in troughs +SH (Fig. 3.3D; Table 3.2).

More specifically, seven taxa were identified in Gabriel biplots as being important in distinguishing among the habitat groupings in the PCA-H analysis of macrofaunal cores (Fig. 3.2A). Taxa contributing to > 5% of CNESS variation included the bivalves *Spisula solidissima*, and *Tellina agilis*, Nemertea spp., the amphipod *Acanthohaustorius* sp., and Oligochaeta spp. (Fig. 3.2A). Two others, the polychaete *Protodrilus* sp. and the amphipod *Politolana polita*, contributed 2 to 5% of the CNESS variation (Fig. 3.2A). Of these only three (those with higher factor loading scores from the PCA-H analysis) were shown to have significant differences in mean density among habitats (Fig. 3.4; Table 3.4). Mean density of *S. solidissima* was significantly greater in ripple troughs (troughs +SH: 6.8 ind. 38.5 cm<sup>-2</sup> and troughs -SH: 7.0 ind. 38.5 cm<sup>-2</sup>) compared to either ripple crests (3.5 ind. 38.5 cm<sup>-2</sup>) or flanks (3.3 ind. 38.5 cm<sup>-2</sup>) (Fig. 3.4; Table 3.4). Mean density of *T. agilis* was significantly greater in ripple flanks (2.3 ind. 38.5 cm<sup>-2</sup>), troughs +SH (2.0 ind. 38.5 cm<sup>-2</sup>), and troughs -SH (2.4 ind. 38.5 cm<sup>-2</sup>) compared to crests (0.6 ind. 38.5 cm<sup>-2</sup>). In contrast, mean density of Nemertea spp. was greatest in ripple crests (5.3 ind. 38.5 cm<sup>-2</sup>), but this difference was only significant when compared to ripple flanks (0.4 ind. 38.5 cm<sup>-2</sup>) (Fig. 3.4; Table 3.4). In terms of general trends, Oligochaeta spp. and *P. polita* had relatively higher densities in ripple troughs -SH, whereas, *Acanthohaustorius* sp. and *Protodrilus* sp. had relatively lower densities in ripple flanks (Fig. 3.5).

### Environmental data

Spatial pattern in PCA analysis of environmental data showed similar clustering of samples based on habitat type to those observed for the macrofaunal data and although

habitat groupings were distinguishable, they were not well separated from each other in “PCA space” (Fig. 3.6). Samples taken from ripple crests were the most distinct, whereas trough samples (+SH and -SH) formed another group. Ripple flank samples again were not a very distinct group and showed considerable overlap with crest and trough samples. Flank samples based on PCA of environmental data were more similar to ripple crests than the PCA-H analysis of macrofaunal samples. Principal components axis 1 was important in distinguishing among the habitat groupings described above and explained 45% of the variation in the data. Variation among samples within-habitats generally occurred along axis 2 and explained 32% of the variation in the data. Fine grained sediment ( $< 250 \mu\text{m}$ ; average %), and particulate organic carbon were heavily weighted positive loadings along axis 1, whereas, medium to coarser grained sediment ( $\geq 250 \mu\text{m}$ ) showed a heavily weighted negative loading along axis 1. Chlorophyll *a* and phaeophytin were heavily weighted positively along axis 2.

More specifically, comparisons of environmental variables among habitats indicated that medium to coarser grained sediment ( $\geq 250 \mu\text{m}$ ) was significantly higher in ripple crests ( $\bar{x}=96.8\pm1.3 \%$ ) compared with flanks ( $94.6\pm2.1 \%$ ), troughs +SH ( $\bar{x}=93.8\pm1.7 \%$ ) and troughs -SH ( $\bar{x}=92.83\pm2.9 \%$ ) (Fig. 3.7A; Table 3.4). Finer grained sediment ( $< 250 \mu\text{m}$ ) was significantly higher in troughs +SH ( $\bar{x}=6.4\pm1.8 \%$ ) and troughs -SH ( $\bar{x}=7.4\pm1.9 \%$ ) compared to either crests ( $\bar{x}=3.4\pm1.4 \%$ ) or flanks ( $\bar{x}=1.3\pm2.2 \%$ ) which also differed significantly from each other, with lower amounts in ripple flanks (Fig. 3.7B ; Table 3.4). Particulate organic carbon was significantly higher in troughs +SH ( $\bar{x}=2.8\times10^{-2}\pm0.38\times10^{-2} \%$ ) and troughs -SH ( $\bar{x}=2.7\times10^{-2}\pm0.16\times10^{-2} \%$ )



compared to either crests ( $\bar{x}=2.4\times10^{-2}\pm0.19\times10^{-2}\%$ ) or flanks ( $\bar{x}=2.3\times10^{-2}\pm0.22\times10^{-2}\%$ ) (Fig. 3.7C; Table 3.4). Phaeophytin was generally higher in troughs (+SH and -SH) compared to ripple crests and flanks, whereas, sediment chl *a* (i.e., benthic diatoms) showed the opposite trend but these differences were not significant (Fig. 3.7 D, E; Table 3.4).

Total density and taxon richness were significantly positively correlated with particulate organic carbon (Table 3.5). Diversity was also significantly positively correlated with phaeophytin. Taxon richness was correlated positively with finer grained sediment and negatively with medium to coarser grained sediment, as was diversity (Table 3.5). Of the taxa important in distinguishing among sample groupings produced from PCA-H analysis, *S. solidissima* and *T. agilis* were significantly positively correlated with particulate organic carbon and phaeophytin respectively. Both *T. agilis* and *P. polita* were significantly positively correlated with finer sediments and negatively with medium to coarser sediments (Table 3.5).

## DISCUSSION

An outstanding feature of soft-sediment macrofaunal communities is that individual abundances and species composition vary greatly at a variety of spatial scales (cm to km). Nested sampling designs have been recommended as a way of characterizing this large variation, and as an aid to understand how community patterns are formed (Morrissey et al. 1992; Ramey and Snelgrove 2003). Since macrofaunal organisms are intimately associated with the sediment in which they live, one would expect strong relationships between sediment properties, and species distributions and abundances, but

this has not been widely examined for a suite of sediment parameters, nor for multiple habitats in sandy continental shelf sediments. In this chapter, an alternative approach to nested designs with blind or remote, random sampling methods was used. Macrofaunal communities were examined within the context of known distributions of multiple topographic habitat features and sediment parameters in an attempt to elucidate variability within an ecological context (e.g., Sisson et al. 2002; Zajac et al. 2003; Barros et al. 2004; Baptist et al. 2006).

The previous chapter demonstrated that topographic habitat features (i.e., ripple crests vs troughs) were instrumental in identifying macrofaunal community patterns in continental shelf sediments over scales of meters to kilometers. Zajac et al. (2003) also found macrofaunal populations exhibited complex and spatially varying patterns of abundance in relation to habitat defined by distinct sediment patches, and biogenic structures at scales ranging from meters to kilometers. Here I present evidence of additional habitat heterogeneity at LEO-15 within the smallest scale examined (i.e., 60 m) in the previous Chapter. Four topographic habitat features including ripple crests, flanks, troughs with shell hash (trough +SH), and troughs without shell hash (troughs – SH) were frequently found within 1 m<sup>2</sup> areas at Sta. 9. Macrofaunal community and sediment related variables in separate PCAs (Principal Components Analyses) produced clusters of samples that corresponded with three of the four defined habitats, rather than corresponding to their spatial arrangement along the transect (i.e., by quadrat). Although the three general habitat clusters were distinguishable, they were not distinctly separated from each other in “PCA space”. This is not surprising given that these habitats were located in close proximity to each other (within 1 m<sup>2</sup> area), in a highly disturbed

environment with no obvious barrier to species dispersal. What is interesting, however, is that samples taken close together within areas  $< 1 \text{ m}^2$  from a ripple crest, flank and trough (+SH and –SH) were more different from each other than from replicate samples from crests, flanks, or troughs taken further apart at distances ranging from 2 to 44 m. Moreover, variation in macrofaunal communities partitioned among habitats (spatial component removed) and among quadrats (habitat component removed) showed that the variance among habitats was almost twice as high as that among quadrats making up 4% and 2% of the total variance fraction respectively.

Community differences were present among crests, flanks, and troughs (includes troughs +SH and –SH) and macrofauna most important in distinguishing among these three habitats included *Spisula solidissima* and Nemertea spp., two of the same taxa important in distinguishing between crests and troughs in the previous chapter, along with the deposit-feeding bivalve, *Tellina agilis*. *Spisula solidissima*, and the deposit feeding bivalve, *T. agilis*, were dominant members of the community in troughs (+SH and –SH), whereas densities of nemerteans were greater in crests, as observed in the previous chapter. *Tellina agilis* was also important in ripple flanks. Although *Polygordius jouinae* did not contribute to  $> 5 \%$  of the CNESS variation in distinguishing among habitats here, as it did in the previous larger scale analyses (Chapter 2), it was present in low abundances, and exhibited similar habitat associations. *P. jouinae* was not present in crests and density in troughs +SH and –SH was  $0.55 \pm 0.82 \text{ ind. } 38.5 \text{ cm}^{-2}$  and  $0.42 \pm$  and  $0.42 \pm 0.67 \text{ ind. } 38.5 \text{ cm}^{-2}$  respectively. Similarity in communities between troughs +SH and troughs –SH in this study is likely due to the fact that shell hash was not present in large quantities and consisted of small shell fragments rather than large pieces of

surfclam valves, which are known to be transient features at LEO-15 (Able et al. 2003). Shell hash was initially hypothesized to provide a different habitat because its presence may affect the hydrodynamic regime in the surrounding sediments (e.g., velocity and turbulence of the benthic boundary layer; Newby 2006), and it may also provide areas of refuge from predators (Kamenos et al. 2004). Further research is necessary to determine whether higher concentrations of large surfclam valves in ripple troughs constitute a different habitat with associated species.

In concert with macrofaunal community patterns, differences in sediment properties (i.e., particulate organic carbon, grain size, chl *a* and phaeophytin) were also associated with particular habitats. In general, sedimentary organic matter and grain size varied among habitats. Ripple troughs (+SH and –SH) contained relatively higher levels of particulate organic carbon (~1.2 times higher) associated with finer sediments, compared with crests and flanks. Following the phytoplankton bloom (i.e., May 2006) concentrations of chl *a* and phaeophytin at Sta. 9 and Node B at LEO-15 have also been shown to be up to five times higher in ripple troughs than in crests (see Chapter 6). The significant role microtopography plays in advective transport of water through the interstices of the sediment has been identified as a key process enhancing the deposition, transport, and patchiness of organic matter in permeable shelf sands (Huettel et al. 1996; Pilditch et al. 1998; Reimers et al. 2004).

In sandy rippled beds, near bottom water containing organic matter and oxygen, is pumped into the sediments in ripple troughs, where organics may become trapped, whereas pore water is pumped out at the apex of crests (Huettel et al. 1996; Ziebis et al. 1996; Huettel and Webster 2001). In oscillatory flows, ripples (0.7 cm height and 3 cm

wavelength) enhanced porewater exchange rates by factors of 6-15 (Precht and Huettel 2003). In an attempt to mimic sediment and hydrodynamic conditions representative of continental shelf environments, Pilditch and Miller (2006) used an oscillatory water tunnel and cultured diatoms as a tracer for particulate organic matter. Results showed greater diatom deposition (3.5 x) and penetration depths (4-5 cm) in ripple troughs than in crests (< 2 cm). Organic matter may also accumulate in troughs by settling there as a result of reduced shear stress.

The main driving forces of advection are pressure gradients along the sediment surface which occur whenever unidirectional or oscillating bottom flows are deflected by topography (Huettel and Gust 1992; Precht and Huettel 2003). Differences in ripple characteristics such as height and wavelength may be important in explaining the spatial variability of infauna and finer scale patchiness in organic matter distribution in sandy continental shelf sediments. In Botany Bay, Australia at 7-8 m depth, Barros et al. (2004) indicated that there may be a relationship between spatial variability of macrofaunal assemblages (500- $\mu\text{m}$  sieve; Family level identification) and the size of ripples, where dissimilarity within replicates (within crests and within troughs) and the dissimilarity among replicates (between crests and troughs) were greater for larger ripples. At LEO-15 current speed, direction, and topography can change on time scales from seconds to seasons and differences in the distribution of food quality measures such as chl *a* and phaeophytin contributed to considerable within habitat variability. Moreover, 90 % of the variance based on taxon composition and abundances was present within cores at scales of  $\leq 38.5 \text{ cm}^{-2}$  and this variability was significantly less than expected from random mixing. Although ripple characteristics were not measured along the transect for

logistical reasons, video and camera images indicated considerable variability in ripple morphology. Some were symmetrical in shape with sharp crests, indicative of sand grains moving shoreward with the wave crest and seaward with the passing of the wave trough. Others were more shallow, with a ripple bed that was irregular and hummocky in appearance.

Only a few species showed significant correlations with sediment properties which may be due to low taxon abundance, frequent disturbance of sediments, small-scale heterogeneity of food resources, combined with the potentially limited small-scale horizontal movements of many macrofaunal species. Basic community measures such as total macrofaunal density and taxon richness, on the other hand, were correlated positively with surrogate measures of food availability and quality (i.e., sedimentary organic carbon and phaeophytin). Sediment grain size was also significantly correlated with taxon richness and diversity, but co-varied with particulate organic matter. There is little evidence that such a narrow range in sediment grain sizes is a key determinant in influencing macrofaunal distributions at such small spatial scales, and concentration of organic matter is a more probable explanation for distribution patterns. However, correlations do not identify causes for the observed patterns and the mechanistic basis for this sort of sediment preference remains poorly understood.

In this Chapter I have shown that community patterns at relatively small scales (i.e., cm to m) can be related to defined topographic features, and sediment properties such as concentration of food resources, such as organic carbon as well as sediment grain size may be important in influencing observed macrofaunal patterns. It is well known that patchiness of resources coupled with the behavior of species can determine the

arrangement of individuals within communities (Thrush et al. 1989) and heterogeneity generated by ubiquitous and persistent topographic habitat features may be an important source of microhabitat specialization and resource partitioning (Hogue and Miller 1981). The importance of active macrofaunal migration and selection for food resources (i.e., sedimentary organic matter) in creating smaller scale patterns requires further examination. This will be addressed in greater detail in Chapter 6.

## CONCLUSIONS

Topographic habitat features including ripple crests, flanks, and troughs +SH and troughs -SH were frequently encountered within 1-m<sup>2</sup> areas at LEO-15. Macrofaunal community patterns (taxon composition and abundance) and sediment properties (organic carbon, chl *a*, phaeophytin, and grain size) were related to three of these habitats namely crests, flanks, and troughs (+SH and -SH), rather than spatial arrangement along the transect. Thus, communities and sediment properties measured within areas < 1-m<sup>2</sup> were more different from each other than from replicate samples taken further apart at distances ranging from 2 to 44 m. Habitat sample groupings were not distinctly separated spatially from each other in PCA analyses, however, given the fact that these habitats are located close together in a highly disturbed environment with no obvious barrier to species dispersal, it is interesting that such patterns existed. Community differences among habitats were driven by differences in the relative abundance of three dominant taxa namely *S. solidissima*, *Nemertea* spp., and *T. agilis*. In terms of sediment properties, troughs (+SH and -SH) contained relatively higher levels of particulate organic carbon (~1.2 times higher) associated with finer sediments, compared to crests and flanks. Food

quality measures such as chl *a* and phaeophytin contributed to considerable within habitat variability ( $<1\text{-m}^2$ ). Basic community measures such as total macrofaunal density and taxon richness were positively correlated with surrogate measures of food availability and quality (i.e., sedimentary organic carbon and phaeophytin) and heterogeneity in organic matter generated by rippled beds may be important in influencing macrofaunal distributions at  $1\text{-m}^2$  spatial scales.



Table 3.1: Nested AMOVAs (Analysis of Molecular Variance) based on both species/taxon composition and abundance showing degrees of freedom, sum of squares=SS, mean square=MS, estimated variance=est. variance, variance fraction and p-values for: A. among core and within-core variance, B. variance partitioned among and within habitats, C. variance partitioned among and within quadrats. p-values are bolded with \* and indicate whether variance components calculated were significantly different from those obtained by random chance.

A

Source variation	df	SS	MS	Est. variance	Variance fraction	p- value
Among cores	46	92.35	2.00	0.084	10%	<b>0.01*</b>
Within cores	662	494.50	0.75	0.747	90%	<b>0.01*</b>
Total	708	586.85		0.831	100%	

B

Source variation	df	SS	MS	Est. variance	Variance fraction	p- value
Among habitats	3	21.18	7.06	0.029	4%	<b>0.01*</b>
Among cores(habitat)	43	71.16	1.66	0.062	7%	<b>0.01*</b>
Within cores	662	494.50	0.75	0.747	89%	<b>0.01*</b>
Total	708	586.85		0.838	100%	

C

Source variation	df	SS	MS	Est. variance	Variance fraction	p- value
Among quadrats	11	33.21	3.02	0.018	2%	<b>0.01*</b>
Among cores(quadrat)	35	59.14	1.69	0.067	8%	<b>0.01*</b>
Within cores	662	494.50	0.75	0.747	90%	<b>0.01*</b>
Total	708	586.85		0.832	100%	

Table: 3.2 Mann-Whitney test for differences in total density, taxon richness (number of spp.), diversity and evenness among ripple habitats (i.e., crests vs. flanks, crests vs. troughs +SH [troughs with shell hash], crests vs. troughs -SH [troughs without shell hash] flanks vs. troughs +SH, flanks vs. troughs -SH and troughs +SH vs. troughs -SH) at  $\alpha=0.05$ . Mann-U values are given to the left of / and p-values to the right. Significant p-values are indicated with \* and bolded.

Habitat comparison	Total density	Richness	Diversity H' (base 2)	Evenness J'
Crest vs. flank ( $n=24$ )	49.5/0.198	57.0/0.410	50.0/0.219	40.0/0.068
Crest vs. trough +SH ( $n=24$ )	64.5/0.671	45.0/0.128	47.0/0.160	69.0/0.887
Crest vs. trough -SH ( $n=24$ )	50.5/0.219	34.5/ <b>0.028*</b>	36.0/ <b>0.039*</b>	60.0/0.514
Flank vs. trough +SH ( $n=24$ )	40.5/0.068	59.0/0.478	59.0/0.478	37.5/ <b>0.045*</b>
Flank vs. trough -SH ( $n=24$ )	22.0/ <b>0.003*</b>	46.5/0.143	64.0/0.671	45.5/0.128
Trough +SH vs. trough -SH ( $n=24$ )	48.0/0.178	59.0/0.478	61.0/0.551	53.0/0.291

Table 3.3: Mann-Whitney test for differences in density of three taxa among habitats (i.e., crests vs flanks, crests vs. troughs +SH [troughs with shell hash], crests vs. troughs –SH [troughs without shell hash], flanks vs. troughs +SH, flanks vs. troughs –SH and troughs +SH vs. troughs -SH), at  $\alpha=0.05$  of taxa contributing to >5% of CNESS variation in Gabriel biplots and also have heavily weighted factor loadings ( $\pm 0.5$ ). Mann-U values are given to the left of the / and p-values to the right. Significant p-values are indicated in bold with \*.

Habitat comparison	<i>Spisula solidissima</i>	<i>Tellina agilis</i>	Nemertea spp.
Crest vs. flank ( $n=24$ )	58.0/0.443	29.0/ <b>0.012*</b>	27.0/ <b>0.008*</b>
Crest vs. trough +SH ( $n=24$ )	32.5/ <b>0.020*</b>	37.0/ <b>0.045*</b>	41.0/0.078
Crest vs. trough –SH ( $n=24$ )	35.0/ <b>0.033*</b>	33.0/ <b>0.024*</b>	48.5/0.178
Flank vs. trough +SH ( $n=24$ )	37.5/ <b>0.045*</b>	52.5/0.266	69.5/0.887
Flank vs. trough –SH ( $n=24$ )	35.5/ <b>0.033*</b>	71.0/0.977	47.5/0.160
Trough +SH vs. trough –SH ( $n=24$ )	67.0/0.799	65.0/0.713	62.0/0.590

Table 3.4: Mann-Whitney test for differences in particulate organic carbon, phaeopigment, chlorophyll *a*, finer grained sediment (<63-250  $\mu\text{m}$ ), and medium to coarser grained sediment ( $\geq 250$ ) among habitats (i.e., crests vs. flanks, crests vs. troughs +SH [troughs with shell hash], crests vs. troughs -SH [troughs without shell hash] flanks vs. troughs +SH, flanks vs. troughs -SH and troughs +SH vs. troughs -SH), at  $\alpha=0.05$ . Mann-U values are given to the left of the / and p-values to the right. Significant p-values are indicated in bold with \*.

Habitat comparison	Carbon (%) <i>n</i> =48	Phaeopig. (mg g <sup>-1</sup> ) <i>n</i> =48	Chl <i>a</i> (mg g <sup>-1</sup> ) <i>n</i> =48	Finer (%) <i>n</i> =44-46	Medium to coarser (%) <i>n</i> =44-46
Crest vs. flank ( <i>n</i> =21-24)	61.0/0.551	57.0/0.410	48.0/0.178	25.0/ <b>0.036*</b>	22.0/ <b>0.020*</b>
Crest vs. trough +SH ( <i>n</i> =20-24)	23.0/ <b>0.004*</b>	61.0/0.551	41.0/0.078	10.0/ <b>0.001*</b>	9.0/ <b>0.001*</b>
Crest vs. trough -SH ( <i>n</i> =23-24)	23.0/ <b>0.004*</b>	69.0/0.887	26.0/0.007	2.0/ <b>&lt;0.0001*</b>	3.0/ <b>&lt;0.0001*</b>
Flank vs. trough +SH ( <i>n</i> =21-24)	18.0/ <b>0.001*</b>	52.0/0.266	67.0/0.799	36.0/0.315	43.0/0.631
Flank vs. trough -SH ( <i>n</i> =21-23)	11.0/ <b>&lt;0.0001*</b>	64.0/0.671	51.0/0.242	28.0/ <b>0.036*</b>	33.0/0.080*
Trough +SH vs. trough -SH ( <i>n</i> =21-23)	47.0/0.16	64.0/0.671	59.0/0.478	42.0/0.254	38.0/0.159

Table 3.5.: Spearman nonparametric correlation of taxa contributing > 2% of CNESS variation in Gabriel biplots with sediment variables including particulate organic carbon, phaeopigment, finer grained sediment (< 250- $\mu\text{m}$ ) and medium to coarser grained sediment ( $\geq$  250- $\mu\text{m}$ ). Correlation coefficients and p-values (*italics*) are given. Significant p-values are indicated in bold with \* ( $\alpha=0.05$ ) and \*\* (at  $\alpha=0.01$ ). Dash indicates no significant correlation.

Taxa	Carbon (%) <i>n</i> =48	Phaeopig. ( $\text{mg g}^{-1}$ ) <i>n</i> =48	Finer (<250- $\mu\text{m}$ ) <i>n</i> =43	Medium to coarser ( $\geq$ 250- $\mu\text{m}$ ) <i>n</i> =43
<i>Spisula solidissima</i>	0.381 / <b>0.008**</b>	-	-	-
<i>Tellina agilis</i>	-	0.290 / <b>0.046*</b>	0.366 / <b>0.016*</b>	-0.342 / <b>0.025*</b>
Nemertea spp.	-	-	-	-
<i>Acanthohaustorius</i> sp.	-	-	-	-
<i>Protodrilus</i> sp.	-	-	-	-
<i>Politolana polita</i>	-	-	-0.375 / <b>0.012*</b>	0.422 / <b>0.005**</b>
Community measures				
Density	0.289 / <b>0.046*</b>	0.363 / <b>0.011*</b>	-	-
Richness	0.319 / <b>0.027*</b>	0.350 / <b>0.015*</b>	+0.398 / <b>0.008**</b>	-0.373 / <b>0.014*</b>
Diversity H	-	0.336 / <b>0.021*</b>	+0.356 / <b>0.019*</b>	-0.357 / <b>0.019*</b>
Evenness J	-	-	-	-

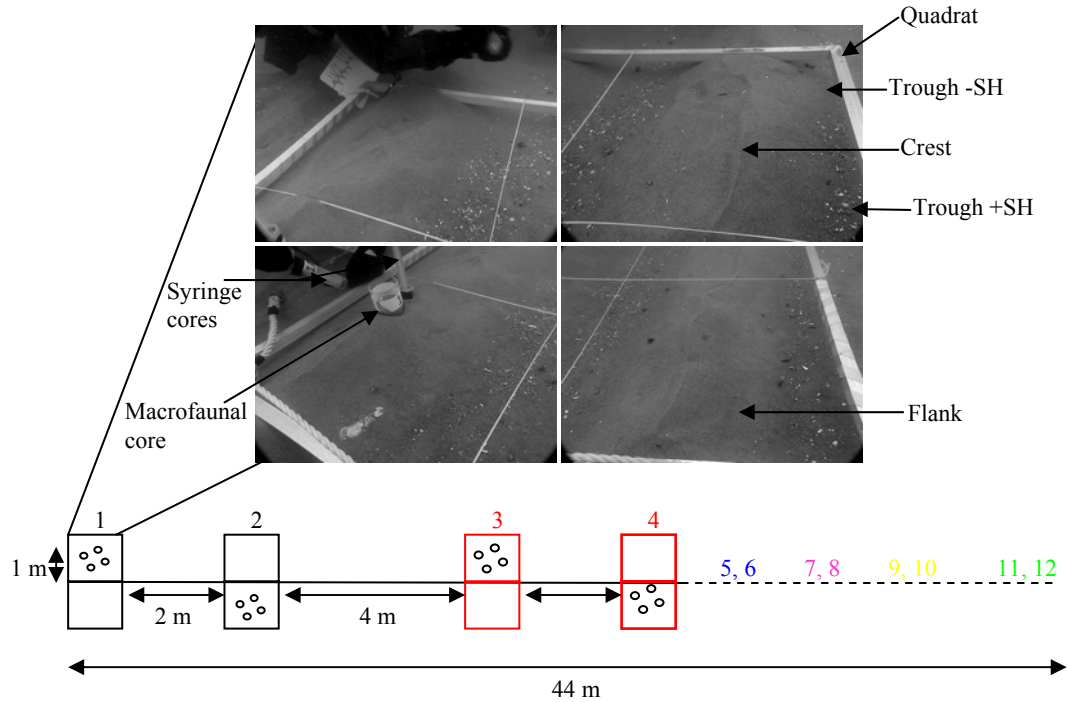


Fig. 3.1. Partially randomized, nested sampling design (spatial scales <1-m, 2-m and 4-m) at Sta. 9 where macrofaunal and sediment score samples were collected from twelve 1 m<sup>2</sup> quadrats on either the left or right side of a 44-m long transect. Four macrofaunal cores and two sediment cores were collected within each quadrat from ripple crests, flanks, troughs +SH, and troughs -SH (macrofaunal core: 1 core habitat<sup>-1</sup> = 4 cores quadrat<sup>-1</sup>,  $n = 48$ ; sediment cores: 2 syringe cores habitat<sup>-1</sup> = 8 syringe cores quadrat<sup>-1</sup>,  $n = 96$ ). Top insert is a digital photograph of quadrat 1 indicating core samples and habitats. Quadrat numbers and colors correspond with those in Figs. 3.2 and 3.6 and indicate where a particular sample was taken along the transect.

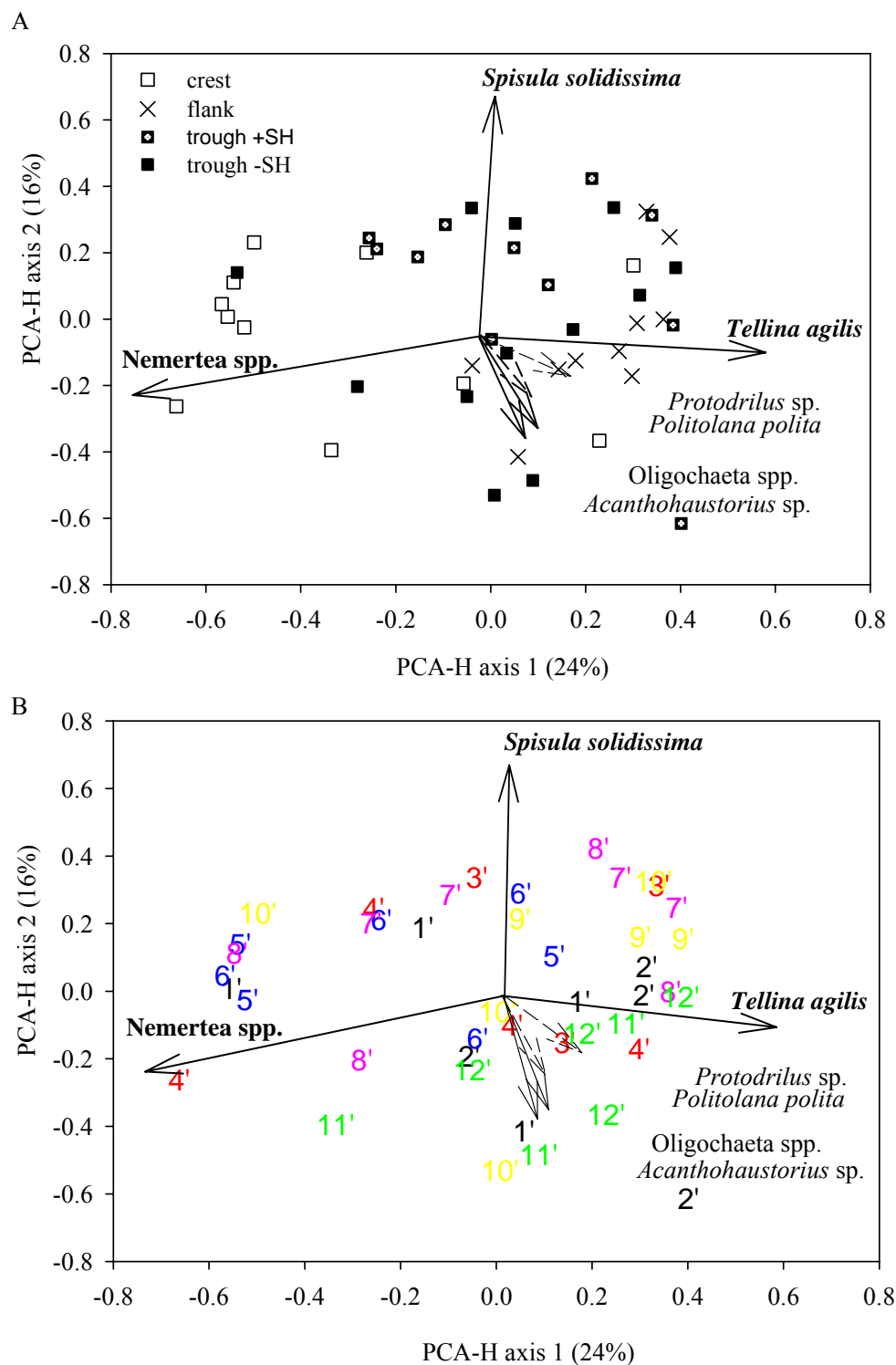


Fig. 3.2. PCA-H metric scaling ordination of macrofaunal core assemblage spatial patterns in June 2005 at Sta. 9 based on CNESS ( $n=5$  individuals). The first two axes

explain 24 and 16% of the variance in the data respectively. Species vectors (Gabriel Euclidean distance biplot) have been overlaid on community ordination to show which species contribute to CNESS variation among samples and therefore drive spatial patterns. Solid and dashed arrows indicate taxa contributing to >5 % and 2-5 % of CNESS variation in biplots respectively. Taxa in bold indicate those with heavily weighted factor loadings ( $\pm 0.5$ ). Individual cores are labeled according to (A) habitat (crest=open square, flank=X, trough with shell hash=square with white circle in the center, and trough without shell hash=filled square, (B) quadrat (numbers and colors correspond to those used in the sampling design shown in Fig. 3.1.



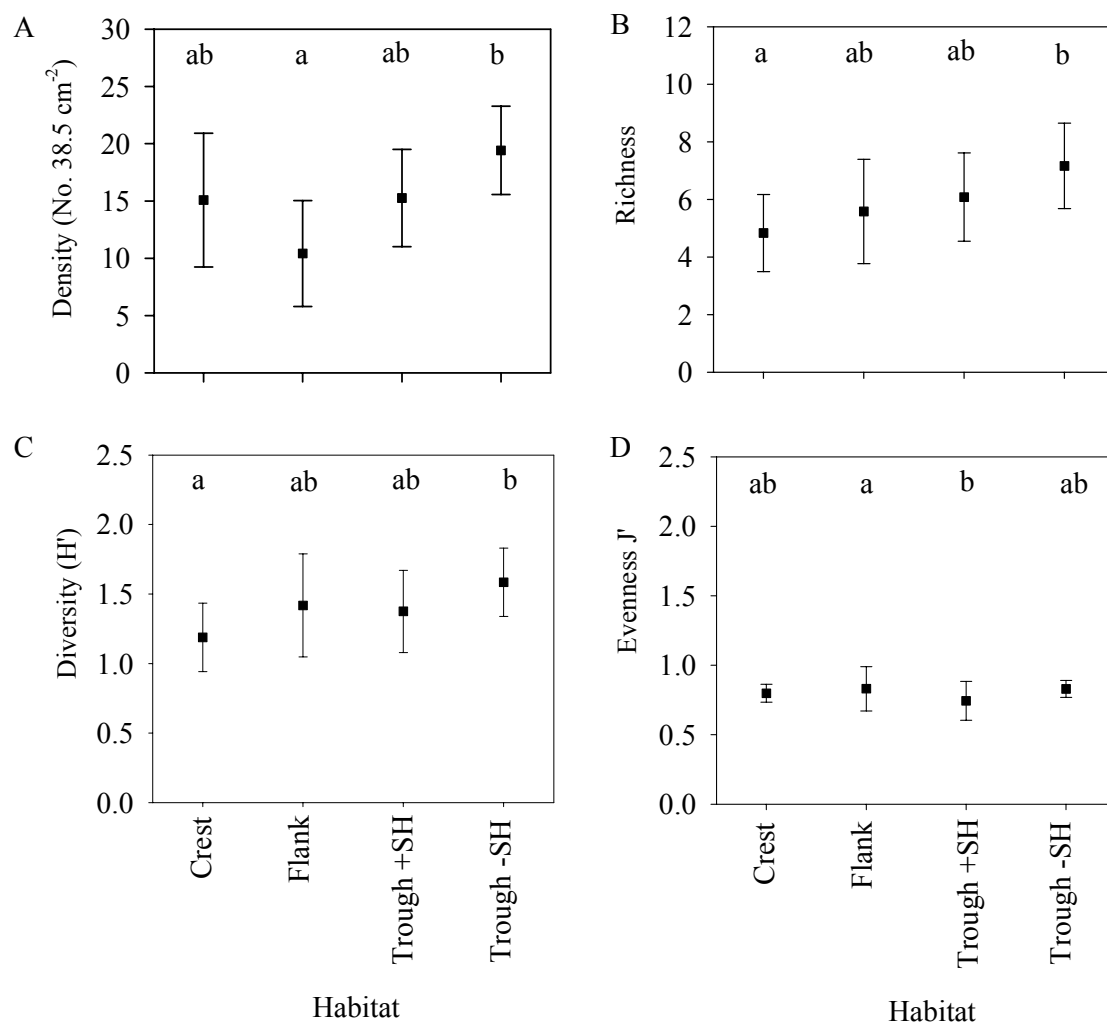


Fig. 3.3. Means  $\pm$  95 % confidence intervals, with  $n=12$  for (A) total density of macrofauna, (B) taxon richness, (C) diversity  $H'$ , and (D) evenness  $J'$ . The same letters (a, b) indicate no significant differences between habitats ( $p > 0.05$ , Mann-Whitney U Test). Note scales on y-axes differ among panels.

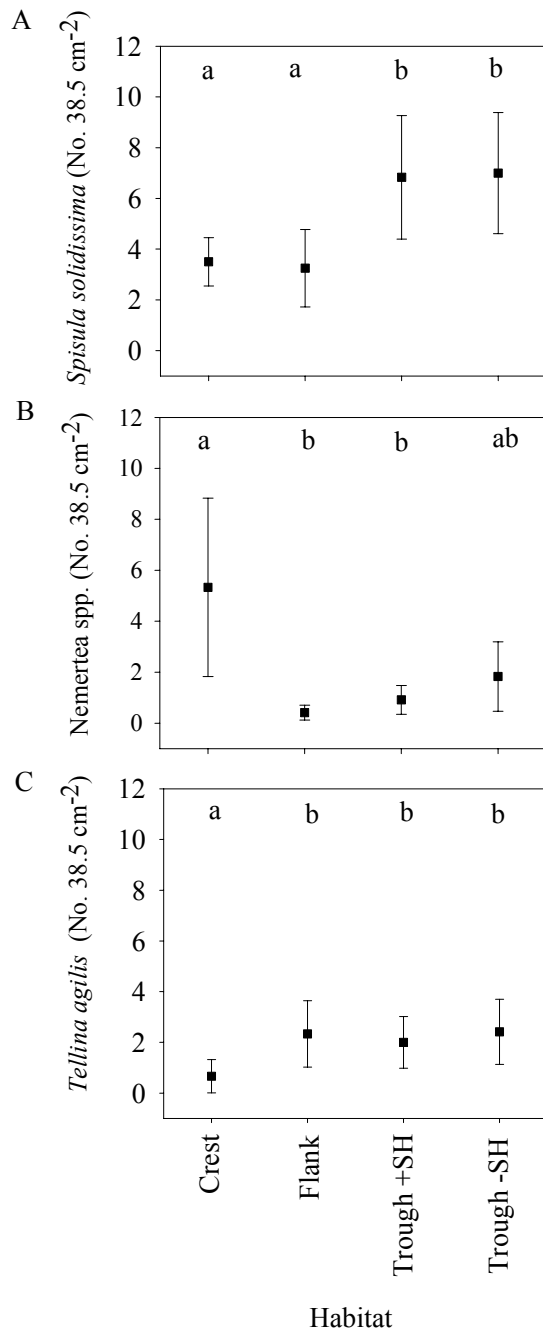


Fig. 3.4. Mean densities  $\pm$  95% confidence intervals, with  $n=12$  of taxa contributing to  $>5\%$  of CNESS variation in Gabriel biplots and also with heavily weighted factor loadings ( $\pm 0.5$ ). The same letters (a, b) indicate no significant differences in density between habitats ( $p>0.05$ , Mann-Whitney U Test)

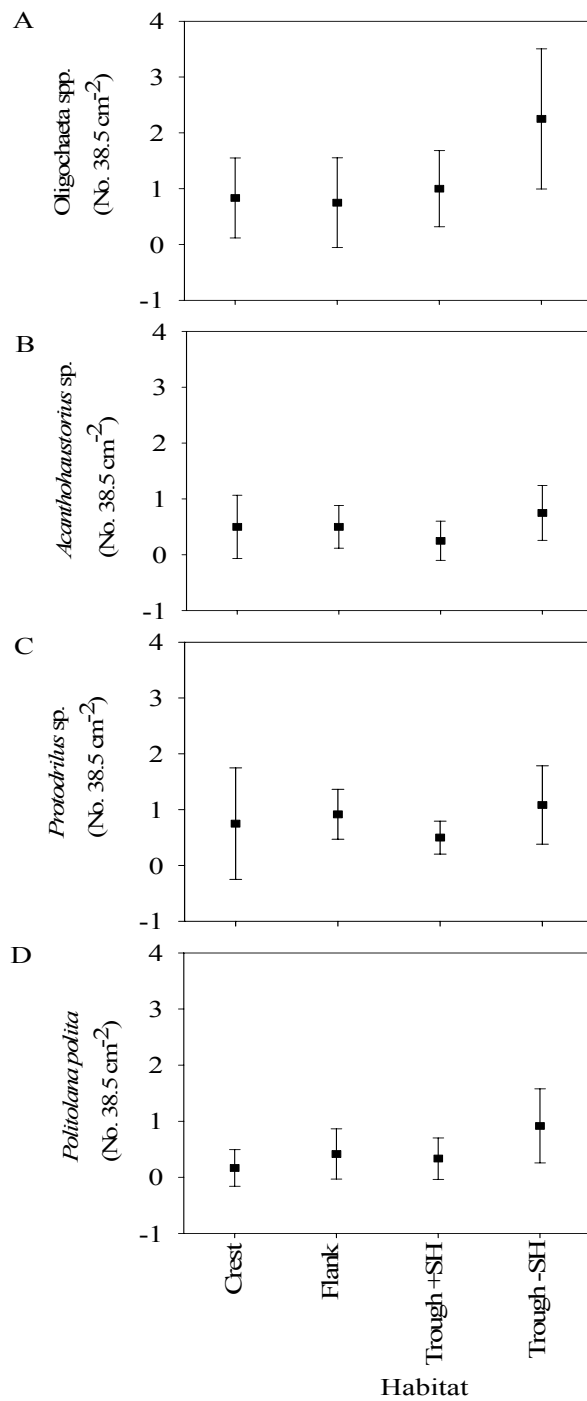


Fig. 3.5. Mean densities  $\pm$  95% confidence intervals, with  $n=12$  of for three taxa contributing to (A and B) >5% and (C and D) 2-5 % of CNESS variation in Gabriel biplots. No significant differences in density among habitats for these taxa ( $p>0.05$ , Mann-Whitney U Test) were found.

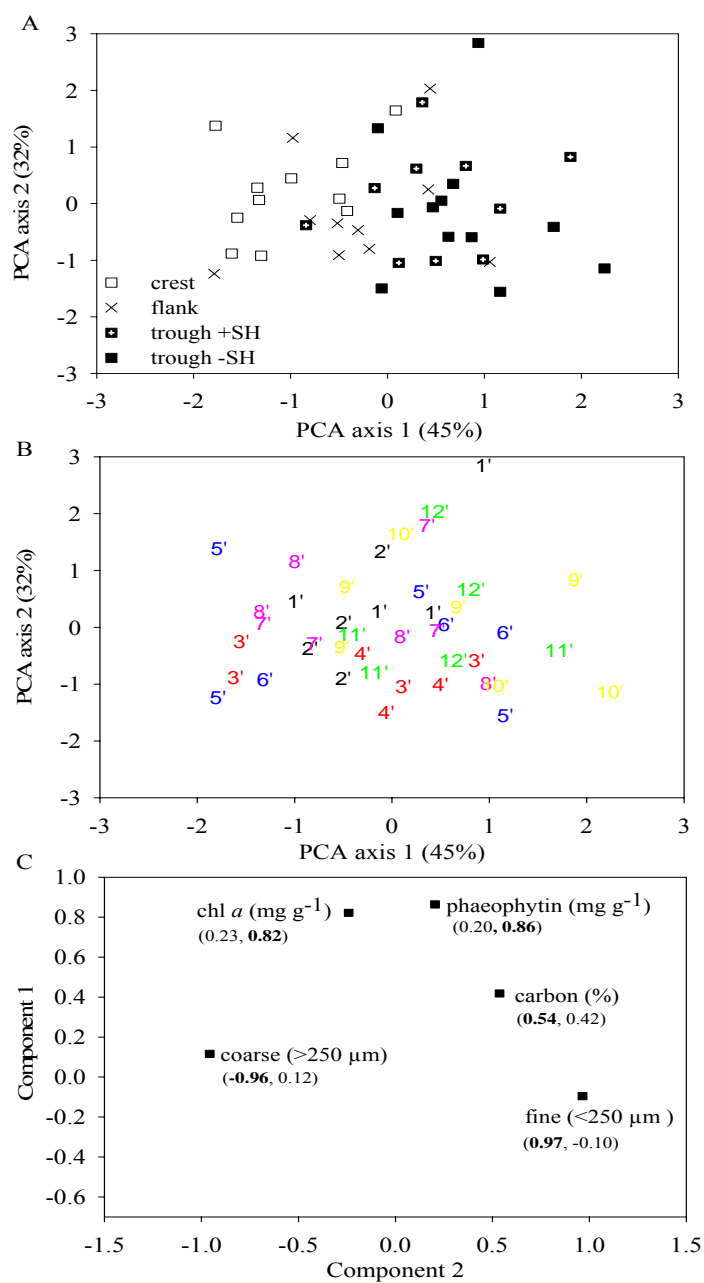


Fig. 3.6. (A, B) Spatial patterns defined by principal components analysis (PCA) of environmental variables. The first two axes explain 45 and 32 % of the variance in the data respectively. Individual cores are labeled according to (A) habitat (crest=open square, flank=X, trough with shell hash=square with white circle in the center, and trough without shell hash=filled square, (B) quadrat (numbers and colors correspond to those

used in the sampling design outlined in Fig. 3.1). (C) Plot of factor loadings for each environmental variable. Heavily weighted loadings ( $\pm 0.5$ ) are bolded.

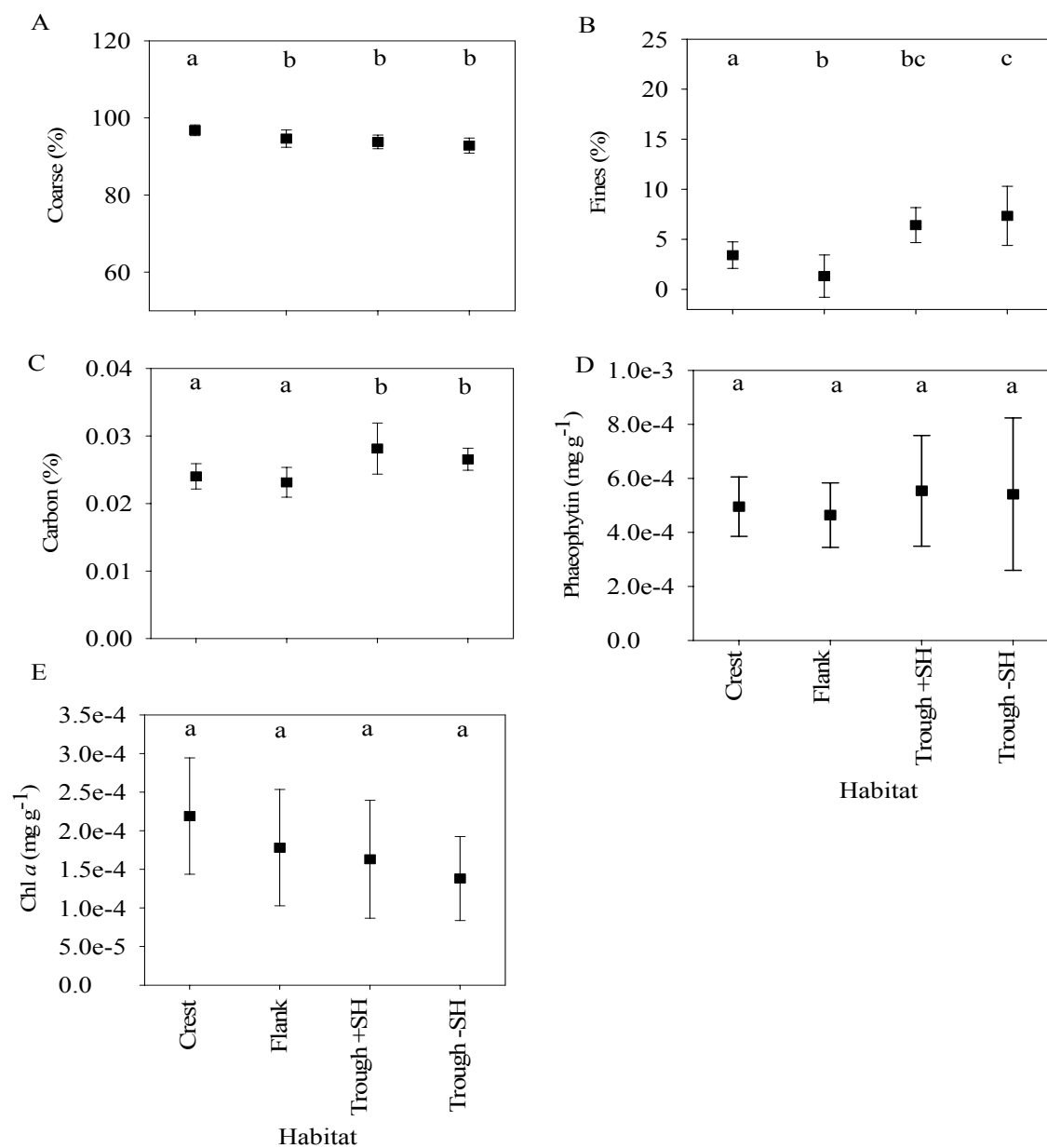


Fig. 3.7. Means  $\pm$  SD for sediment variables, with  $n=10-12$  (A) medium to coarse grained ( $\geq 250$ ), (B) finer (grain sizes  $< 250\text{-}\mu\text{m}$ ), (C) carbon, (D) phaeophytin and (E) chlorophyll *a*. The same letters (a, b) indicate no significant differences in concentration between habitats ( $p>0.05$ , Mann-Whitney U Test). Note scale on y-axes differ among panels.

## CHAPTER 4

# **A NEW SPECIES OF *POLYGORDIUS* (POLYCHAETA: POLYGORDIIDAE): A DOMINANT MEMBER OF INFAUNAL COMMUNITIES ON THE INNER CONTINENTAL SHELF AND IN BAYS AND HARBORS OF THE NORTHEASTERN UNITED STATES**

## INTRODUCTION

Members of the Polygordiidae Czerniavsky, 1881 are commonly found in intertidal and shallow subtidal sandy sediments, but have also been reported from depths of 152 m on the continental shelf (based on material from the Smithsonian Institution, Washington, DC; Maciolek and Grassle 1987). They are small (length 10-100 mm; width <1 mm), have indistinct segmentation, and lack certain defining polychaete characters such as parapodia and chaetae (except *Chaetogordius canaliculatus* Moore, 1904), but they do have well developed nuchal organs. Members of the Polygordiidae have been found in the Atlantic, Indian, Pacific, and Antarctic Oceans and most are described from European waters (Rouse and Pleijel 2001). Fifteen species and two subspecies have so far been described in the genus *Polygordius* Schneider, 1868. According to Hartman (1959) other described genera synonymous with *Polygordius* include *Rhamphogordius* Rathke, 1843, *Linotrypane* McIntosh, 1875, and *Pseudogordius* Czerniavsky, 1881. The only other genus in the Family Polygordiidae was established for *Chaetogordius canaliculatus* described by Moore (1904), which was based on fragmented material collected off Cape Cod, USA. This species has never been found again and is generally regarded as an invalid taxon (Hermans 1969; Westheide 1990; Rota and Carchini 1999). The new species, *Polygordius jouinae* sp. nov., is the first *Polygordius* species described from

North America. Although undescribed to this date, the present study shows that it has been collected before (referred to as *Polygordius* sp. or *Polygordius* sp. A) and is a dominant member of sandy macrofaunal communities on the continental shelf and in bays and harbors of the northeastern United States (e.g., Maciolek and Grassle 1987; Snelgrove et al. 2001; Kropp et al. 2002; Battelle 2003, 2004; Maciolek et al. 2004). On the continental shelf off New Jersey, *P. jouinae* sp. nov. at times makes up >50% of the macrofauna in sandy sediment communities with densities as high as 98,400 individuals m<sup>-2</sup> (Snelgrove et al. 2001). Little is known about the ecology of *P. jouinae* sp. nov., or of the Polygordiidae in general (Rouse and Pleijel 2001). A greater understanding of the natural history and reproductive biology of this species is needed if we are to understand observed spatial and temporal patterns. The present study describes this new species including its 18S SSU rDNA sequence, summarizes its distribution by looking at unidentified material (*Polygordius* sp. and *Polygordius* sp. A) collected along the east coast of the United States, and provides information on the species' reproductive biology, circulatory system, habitat preferences, and ecological importance.

## MATERIALS AND METHODS

### Collection of *Polygordius jouinae* sp. nov.: LEO-15 research site

Specimens for the species description and examination of reproductive biology were collected from Station 9 at the LEO-15 research site (Von Alt and Grassle 1992) on Beach Haven Ridge (39° 27.69' N, 74° 15.81' W) (Fig. 4.1). Beach Haven Ridge (5 km long by 1.5 km wide) is one of 71 shore oblique, sand ridges on the continental shelf off New Jersey (McBride and Moslow 1991). Station 9 is on the shoreward side of the ridge



at ~ 12-m depth, and is a coarse sand habitat (~ 0.5 mm) (Craghan 1995). Samples were collected during spring and summer 2004/2005 by SCUBA divers using 7-cm-diameter corers (surface area 38.5 cm<sup>2</sup>) pushed ~ 10 cm into the sediment. Samples were sorted prior to fixation (live sorted) for *P. jouinae* sp. nov. which were either frozen at -80°C for DNA analysis or fixed in 10% buffered formalin unless indicated otherwise, and transferred to 80% ethanol after 24 h. Fixed material was also obtained through loans from various benthic surveys that have collected *P. jouinae* sp. nov. from bays and harbors along the east coast of the United States including Georges Bank, Massachusetts Bay, Cape Cod Bay, Rhode Island Sound, and Belmar (New Jersey).

#### Belmar research site and habitat data

Infaunal samples from Belmar were collected by the New Jersey Division of Fish and Wildlife (NJDFW) in an independent study examining the impact of sand dredging on macrofauna (1996-2004, unpublished). *Polygordius jouinae* sp. nov. abundance and grain size data obtained by the NJDFW were examined in the present study. Belmar is located ~ 72 km north of LEO-15 and samples were collected from a reference site (~ 1.36 km x 2.04 km), on the continental shelf (~ 40° 11.09' N, 73° 57.08' W) at depths of 13-16 m. This site was divided into six sub-sites (~ 0.68 km x 0.68 km), and within each of these, six infaunal, and one sediment core for grain size were collected seasonally when possible. Corers used in the NJDFW study were the same as those used in the LEO-15 sampling and taken by the same divers. Sorting and identification of samples were completed by the Cove Corporation, Lusby, Maryland. Sediment samples were dried and sieved over nested sieves into eight grain size categories. To determine if there was a

relationship between grain size and density of *Polygordius jouinae* sp. nov. Spearman rank correlations were calculated based on data provided by the NJDFW for the eight sediment grain size categories and density of *P. jouinae* sp. nov. ( $\alpha$  0.05 or 0.01; total= 92). Percent abundance of *P. jouinae* sp. nov. of total macrofauna was calculated for each sub-site/date (total= 134).

#### Light and electron microscopy

Live and fixed specimens collected from LEO-15, New Jersey were studied using stereo and compound microscopes. Measurements were made on fixed material using a high resolution 1.4 megapixel, color firewire camera with Image Pro Express manual measurement software. Total length was measured from the anterior margin of the prostomium (antennae not included) to the posterior margin of the pygidium containing the anus. Prostomium length was defined as the distance from the anterior margin of the prostomium to the head fold (Rota and Carchini 1999). The width was taken at approximately the widest segment in the middle region of the body. Segmentation in preserved specimens is not visible externally making observations of whole, live specimens under a compound microscope essential for counting segments.

Scanning electronic microscopy (SEM) was conducted to confirm certain observations such as the absence of pygidial glands. Worms were fixed using an OsO<sub>4</sub> vapor/OsO<sub>4</sub> + glutaraldehyde protocol while in a Swinnex filter holder (Leander et al. 2003). SEM was also conducted on formalin-fixed material from Massachusetts Bay, Rhode Island Sound, and Belmar. All SEM specimens were dehydrated using a graded ethanol series, critical-point dried using CO<sub>2</sub>, mounted on aluminum stubs, and sputter

coated with gold-palladium (Au-Pd). Stub-mounted specimens were examined with either a Hitachi S4700 SEM or a CamScan CS 24 SEM configured with Orion 5.08 software.

#### DNA extraction and PCR amplification

Worms were sent to Dr. B. Leander for DNA extraction and PCR amplification to determine the 18S small subunit (SSU) rRNA gene from *P. jouinae* (see Ramey et al. 2006 for details on procedures used).

#### Comparative material examined

Type material: *Polygordius antarcticus* Rota and Carchini, 1999: paratype (SMNH 5043), Antarctic Ocean, Ross Sea, Terra Nova Bay, sea between Tethys Bay, 74° 40' S, and Adélie Cove, 74° 46' S, between longitudes 164° 01' E and 164° 08' E, 50 m, leg. G. Carchini, 24 January 1988. *Polygordius eschaturus brevipapillosus* Jouin and Rao, 1987: holotype (MNHN 1392) and paratype (MNHN 1164), Indian Ocean, North Andaman Island, south island beach, 12° 58' 06" N 92° 59' 17" E, 5 cm below surface, near low water mark, sandy sediment (400-700 µm), leg. G. C. Rao, 28 April 1974. *Polygordius pacificus floreanensis* Schmidt and Westheide, 1977: holotype (ZMH P-13668), South Pacific Ocean, Galapagos Islands, Floreana, black beach, eulittoral, coarse black lava sand, leg. June 1972.

Non-type material: *Polygordius appendiculatus* Fraipont, 1887: 15 specimens (NMW 1989.104.1867), north-eastern Atlantic Ocean, Irish Sea, St. Georges Channel, 52° 05.7' N 05° 33.7' W, 112 m, sandy gravel, leg. 12 July 1989. *Polygordius jouinae* sp. nov.,

north-western Atlantic Ocean, United States: numerous specimens (USNM 1008249), George's Bank (United States shelf/slope break), 40° 27' 06" N 06° 73' 72" 4" W, 152 m, leg. 10 May 1982, as *Polygordius* sp. A. (Blake et al. 1983; Maciolek and Grassle 1987); – numerous specimens, Massachusetts Bay, leg. August 2004, as *Polygordius* sp A. (Kropp et al. 2002; Maciolek et al. 2004), received from J. Blake, ENSR Marine and Coastal Center; – 7 specimens on slides (MNHN MA22-28), leg. 1967-69, and 3 specimens on slides (YPM : 35707, 35708, 35709), leg. 1967-69, Cape Cod Bay, all as *P. triestinus* Hempelmann, 1906 (det. C. Jouin-Toulmond); – numerous specimens, Rhode Island Sound, sandy sediments, leg. 29-30 July 2003, as *Polygordius* sp A., det. Cove Corporation (Battelle 2003; 2004); – numerous specimens, New Jersey, Belmar on the continental shelf, 40° 11.09' N 73° 57.08' W, leg. 2001, as *Polygordius* sp., det. Cove Corporation, New Jersey Division of Fish and Wildlife; – numerous specimens, New Jersey, Beach Haven Ridge, LEO-15, 39° 27.69' N 74° 15.81' W, leg. August to September 1994, as *Polygordius* sp., det. R. Petrecca (Snelgrove et al. 1999; 2001), received from F. Grassle, IMCS Institute Marine and Coastal Sciences, Rutgers University. *Polygordius lacteus*: 1 specimen (USNM 53318), north-western Atlantic Ocean, United States, Maine, nearest place Crow Neck, North Tresscott, 0-1 m, leg. 20 February 1976, det. N. Riser; – 1 specimen (SMF 9842), north-eastern Atlantic Ocean, France, Roscoff in Brittany, leg. in the 1970s. *Polygordius neapolitanus*: numerous specimens (MNHN), Mediterranean Sea, Italy, Naples, leg. Dius, 10 May 1907; – 3 parts (BMNH 1928.4.26.657/8), leg. Fauvel, 26 April 1928.

### List of abbreviations

BMNH The Natural History Museum, London; MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MNHN Muséum National d'Histoire Naturelle, Paris; NBI National Benthic Inventory, Charleston, South Carolina; NMW National Museum and Gallery of Wales, Cardiff; USNH National Museum of Natural History, Smithsonian Institution, Washington DC; SMF Senckenberg Museum, Frankfurt/Main; SMNH Swedish Museum of Natural History, Stockholm; YPM Yale Peabody Museum of Natural History, Yale University, New Haven, Connecticut; ZMB Museum für Naturkunde der Humboldt-Universität, Berlin; ZMH Zoologisches Museum der Universität Hamburg, Hamburg.

## RESULTS

### Type material

Holotype: deposited at YPM (YPM 38050, a complete, sexually mature male, fixed in 80% ethanol, northwestern Atlantic Ocean, United States, New Jersey, Tuckerton, Beach Haven Ridge, LEO-15 station 9 (39°28' N, 74°15' W), ~12 m depth in coarse sand (~ 0.5 mm), leg. P.A. Ramey, 19 May 2005. – Paratypes: six specimens, leg. P. A. Ramey in May 2004/05, at same locality as holotype. Two paratypes deposited at the SMF (SMF 15970 SEM stub No. 679, leg. 27 May 2004; SMF 15971, male, fixed in 80% ethanol, leg. 19 May 2005), one each at YPM 38051 (SEM stub, leg. 27 May 2004), USNM 1086654 (male, fixed in 80% ethanol, leg. 19 May 2005), NBSC V3709 (female, fixed in 80% ethanol, leg. 19 May 2005), and MCZ 68620 (male, 80% ethanol, leg. 19 May 2005).

### Diagnosis

Prostomium conical with two tapering antennae attached close together at their bases. Ratio of antenna length to prostomium length is ~1:1. Eyes absent. Pygidium densely ciliated, with terminal anus with seven small lobes directed interiorly. Pygidium not inflated and without glands or anal cirri. Species gonochoristic.

### Description (based on holotype)

Sexually mature male, clear to milky white in color (live observation) due to presence of sperm. Opaque after fixation. Body elongated (length=19.4 mm) and cylindrical, tapering towards the head and terminal anus. A distinctive ventral groove present. All segments lacking parapodia and achaetous. Prostomium and peristomium separated by a ventral transverse groove or “head fold” (Fig. 4.2A). Prostomium conical (length=140  $\mu$ m) with two tapering antennae (length=130  $\mu$ m) attached very closely at their bases (Fig. 4.2A). Antennae with sensory cilia. Length ratio of antenna to prostomium ~1:1 (Fig. 4.2A; Table 4.1). One pair of oval, heavily ciliated nuchal organs present dorsolaterally, at the posterior margin of the prostomium (Fig. 4.2A). Eyes absent. Mouth ventral with densely ciliated buccal lip (Fig. 4.2A-D). Posterior end not inflated, and without pygidial glands or anal cirri (Fig. 4.2E-F). Pygidium densely ciliated with a terminal anus with seven small lobes directed interiorly (Fig. 4.2F). External segmentation not visible. Number of segments inconclusive (>65) due to fixation and subsequent opaqueness. Complete segment counts determined for other sexually mature individuals mounted live on slides (see Table 4.1). Internal segmentation best visible in live, sexually mature individuals with blood sinuses enlarged thus providing a reddish

hue. Body widest in mid-region (width=0.23 mm). Body surface covered by thin cuticle with fine transverse striations (Fig. 4.2G), perforated with many small irregularly distributed oval pores (length  $\sim 1 \mu\text{m}$ ; width  $0.5 \mu\text{m}$ ) (Figs. 4.2G, H). Variability in measurements in sexually mature specimens: antenna and prostomium length 0.11 to 0.15 mm, body length 13.0 to 43.1 mm, body width 0.23 to 0.38 mm, number of segments 82 to 93 (see also Table 4.1). No evidence of sexual dimorphism in this species (see Table 4.1 for female vs male measures). Information pertaining to distribution, habitat, reproduction, and circulatory system addressed below based on additional paratype and non-type material. SSU rDNA sequence from *P. jouinae* sp. nov. deposited in GenBank (Accession number DQ153064) containing 8 novel indels at positions 250, 711, 775, 851, 857, 884, 895, and 1732 (relative to the pairwise aligned sequence 'AF412809').

#### Distribution and habitat

Spearman rank correlations of sediment grain size with density (individuals  $\text{m}^{-2}$ ) of *P. jouinae* sp. nov. collected at Belmar showed that density was significantly ( $p < 0.05$ ;  $n=92$ ) positively correlated with the proportion of medium to very coarse sand (0.25-1.00 mm) and negatively correlated with the fine sand (0.125-0.25 mm) fractions (Table 4.2). *Polygordius jouinae* sp. nov. was present at all sub-site/dates from 1996-2003, (with the exception of three sampling dates) and comprised up to 78 % (mean=27%) of the total macrofaunal abundance (individuals  $\text{m}^{-2}$ ).

## Reproduction

*Polygordius jouinae* sp. nov. collected on 19 May 2004 and 27 May 2005 from the LEO-15 research site comprised only sexually mature individuals. The proportion of males to females was ~ 1:1. Both sexes were notably swollen with gametes and had enlarged blood sinuses giving them a reddish hue when viewed with the naked eye. Oocytes were tightly packed in the coelom and appeared clear and irregular in shape (Fig. 4.3A). They were present from the first 19-27 segments until the last 10-16 and moved freely throughout the coelom. It is likely that oocytes and sperm are set free by rupture of the body wall (Fig. 4.3B). Released from the body cavity, oocytes were rounder and varied in size (diameter 22-62  $\mu\text{m}$ ). Males were milky white in appearance and sperm were present from the first 15-25 segments until the last 10-20. Spermatozoa had round heads (3.30-3.56  $\mu\text{m}$ ), tiny pointed acrosomes, short mid-pieces, and long tails (50-60  $\mu\text{m}$ ), (Fig. 4.3C-D).

## Circulatory System

The dorsal blood vessel divides in front of the mouth to form two lateral loops (referred to as circumoesophageal blood commissures in Fig. 4.4., Rota and Carchini 1999) which enter the prostomium and then loop back towards the posterior part of the peristomium to join the ventral blood vessel (Fig. 4.4A, B). Beginning near the posterior peristomium, intersegmental blood commissures run from the dorsal blood vessel to the ventral blood vessel. In the foremost segments (i.e. first 20 or so) these intersegmental blood commissures form long loops positioned ventrolaterally (Fig. 4.4C). In the genital



segments smaller blood vessels oriented antero-posteriorly appear to end blindly as described in *P. triestinus* sensu Jouin 1970 (Fig. 4.4D).

#### Gut parasites

Stereomicroscopic observations of live *Polygordius jouinae* sp. nov. from LEO-15 revealed that the intestines were heavily infected with single-celled, ovoid parasites within the gut. This parasite is gregarine-like and may be closely related to the intestinal parasites reported for *P. antarcticus* and for another species, *P. neapolitanus* Fraipont, 1887. A separate study of the intestinal parasites was completed (Leander and Ramey 2006).

### DISCUSSION

*Polygordius jouinae* sp. nov. is distinguished from most other *Polygordius* species by its non-inflated, heavily ciliated pygidium, the absence of pygidial glands, and conical (rather than rounded) prostomium. Morphologically similar species include *Polygordius triestinus* Hempelmann, 1906 from the North Adriatic Sea, *Polygordius triestinus* sensu Jouin (1970) from New Caledonia, and *P. antarcticus* Rota and Carchini, 1999 from the Ross Sea, Antarctic Ocean. However, *Polygordius jouinae* sp. nov. can be clearly distinguished from the three species mentioned above by the following characters (see also Table 4.1). *Polygordius jouinae* sp. nov. is gonochoristic, whereas Hempelmann's *P. triestinus* is hermaphroditic, described as having oocytes and sperm in close proximity to each other in the coelom (Hempelmann 1906). Currently *P. triestinus* is the only known hermaphroditic species in the Polygordiidae, however, hermaphroditism cannot be ruled out for *P. triestinus* sensu Jouin, as only sexually mature males were found. *Polygordius jouinae* sp. nov. lacks the pygidial glands, whereas they are present in *P. triestinus* sensu

Jouin and *P. antarcticus*. *P. jouinae* sp. nov. also lacks an inflated pygidium present in *P. antarcticus*. Additionally the length ratio of antenna to prostomium is 1:1 for *P. jouinae* sp. nov. in contrast to 0.5:1 in *P. antarcticus*.

Unfortunately, direct comparison of holotypes was impossible since specimens of *P. triestinus* sensu Jouin (1970) were not deposited in Paris (MNHN) and are not available in the personal collection of C. Jouin (C. Jouin-Toulmond, pers. comm.). As in the present study, Rota and Carchini (1999) were unsuccessful in locating type material for *P. triestinus*. They also reported that specimens were not present in the Laboratory of Marine Biology, Trieste. Since Hempelmann and Woltereck, who provided Hempelmann with the original specimen(s) for the description of *P. triestinus* and therefore was often erroneously quoted as author of this taxon (for history of the name see Ramey et al. 2006), both worked at the University of Leipzig, Germany, type specimens were also requested from several German collections including Berlin (ZMB), Hamburg (ZMH), and the Senckenberg (SMF). However, these requests were unsuccessful. Furthermore, *P. triestinus* has not been reported in benthic samples from the Gulf of Trieste from 1966 to 2003 (V. Solis-Weiss, pers. comm.). Unfortunately, the loan request to the Museo Civico di Zoologia di Roma, Rome, for the holotype of *P. antarcticus* remained unanswered.

In addition to the distinction based on morphological characters, especially in a polychaete taxon lacking ‘typical’ characters such as chaetae and parapodia, the 18S ribosomal RNA sequence from *P. jouinae* sp. nov. was determined and deposited in GenBank as a reference for further systematic studies of this group. Furthermore, the 18S ribosomal RNA sequence from *P. jouinae* sp. nov. (Accession number DQ153064) was compared to the sequence from an unnamed *Polygordius* species collected from Anse

Forbans and Mahé, Seychelles, India (Accession number AF412809; Struck et al. 2002), which was also deposited in GenBank. The sequence from *P. jouinae* sp. nov. was 98.2% identical to the sequence from the *Polygordius* sp. from India (32 differences over 1814 compared sites), however, it contained eight novel indels at positions 250, 711, 775, 851, 857, 884, 895 and 1732 (relative to sequence AF412809), thus adding to the distinction of *P. jouinae* sp. nov.

Rota and Carchini (1999) summarized the characters previously used to identify species of *Polygordius* such as body size, segment number, color, shape of pygidium, ciliation on the body surface, pattern of the circulatory system, etc. (Rota and Carchini 1999: Table 4.1). During the present study, observations on living and fixed material of *Polygordius jouinae* sp. nov. showed that color differs depending on whether specimens are live or fixed, or sexually mature males or females. In sexually mature individuals the oocytes and sperm packed into the coelom greatly influence body width leaving external segmentation invisible thus making it difficult to count segments in preserved material. Identifications based on differences in the arrangement of the circulatory system have been controversial (Rota and Carchini 1999) and this character is considered of limited diagnostic value. Moreover, species for which the circulatory system has been discussed include different levels of detail, are fraught with inconsistent terminology, and re-evaluation in specimens that have been preserved for a long time proved very difficult. In the present study of specimens of *P. jouinae* sp. nov. features of the circulatory system, specifically the vascular loops connecting dorsal and ventral vessels in the anterior part of the body, proved very similar to those observed for *P. triestinus* sensu Jouin (1970) (based on personal notes kindly provided by Dr. Jouin-Toulmond) and those reported for

*P. antarcticus* by Rota and Carchini (1999). Specimens collected from Cape Cod Bay, Massachusetts in 1968-69 had been identified as *Polygordius triestinus* by Dr. C. Jouin-Toulmond in the 1970's based primarily on details of the blood vascular system as described by Hempelmann (1906) for the respective species. However, she also noted that this species was gonochoristic. Our careful re-examination of these Cape Cod specimens, which had been deposited in the collections of the Yale University (YPM) as well as at the Muséum National d'Histoire Naturelle (MNHN), considering reproductive mode (gonochorism/hermaphroditism), additional features of the pygidium such as overall shape (inflated/non inflated) and the presence/absence of pygidial glands, revealed that these specimens belong to *P. jouinae* sp. nov. Thus, *P. jouinae* is named after Dr. Claude Jouin-Toulmond. We agree with Rota and Carchini (1999) that it is likely that many more species of *Polygordius* remain to be described and that the pygidium and its associated structures will be important defining characters. Especially the shape and number of anal lobes can be useful (Ramey and Fiege 2007), although SEM is needed for accurate observation and counting.

Specimens referred to as *Polygordius* sp. or *Polygordius* sp. A in several studies are here referred to *P. jouinae* sp. nov. (i.e. Blake et al. 1983; Maciolek and Grassle 1987; Snelgrove et al. 1999, 2001; Kropp et al. 2002; Battelle 2003, 2004; Maciolek et al. 2004). Samples examined in the present study showed that *P. jouinae* is present in habitats on the inner continental shelf, and in bays and harbors from Massachusetts to New Jersey (42° N and 39° N) to a maximum depth of 152 m on Georges Bank. Macrofaunal samples collected seasonally from six sub-sites at Belmar over eight years showed *P. jouinae* sp. nov. to be the most abundant macrofaunal species in sandy

sediment communities. This dominance in sandy sediments is not restricted to Belmar. In Boston Harbor, *P. jouinae* sp. nov. made up 98% of the macrofaunal (300- $\mu$ m sieve) abundance at a single sandy site with a mean density of 7483 individuals  $\text{m}^{-2}$  (Kropp et al. 2002), and the same trends were found in Rhode Island Sound (area E) where it was the most abundant species in sediments composed of 85-98 % sand (Battelle 2003). In the same location, sediments containing >20 % mud (<0.063 mm) were dominated by a deposit feeding bivalve, *Nucula annulata* Hampson, 1971 (Battelle 2003). On Georges Bank, *P. jouinae* sp. nov. was one of the 10 most abundant species present seasonally at 14 out of 17 regional stations (~80-152 m deep). At shallower locations (stations 1, 4, 10; all 60 m deep) with coarser sediments it was the dominant macrofaunal species (Maciolek and Grassle 1987). The habitat where *P. jouinae* sp. nov. was found is most similar to the habitat of *Polygordius triestinus* sensu Jouin, which was reported from a depth of 6-7 m in an area with strong currents. Bottom sediments were described as medium sand with some fine material, however this area was also susceptible to variable salinities (Jouin 1970). *P. triestinus* is the only *Polygordius* species reported from muddy, oxygen poor sediments in relatively quiescent environments (Hempelmann 1906). *P. antarcticus* was reported from medium to coarse grained, well-oxygenated sands at depths ranging from 31-61 m (Rota and Carchini 1999).

The widespread distribution of relatively high densities of *Polygordius jouinae* sp. nov. in coarse sandy sediments may be related in part to its mode of reproduction. The coelomic spaces of mature *P. jouinae* sp. nov. from LEO-15 were packed with large numbers of small oocytes ( $n$ =several 1000; diameter <63  $\mu$ m) or sperm. Sperm structure indicated that gametes are most likely freely spawned into the water column (Rouse and

Jamieson 1987) and small eggs usually give rise to planktotrophic larvae (e.g., Strathmann and Strathmann 1982). Moreover, planktotrophic larvae occur in the four species of *Polygordius* where development mode is known (Rota and Carchini 1999). In contrast, brooding with direct development of a limited number of eggs is prevalent in interstitial polychaetes (e.g., Spioninae, Fabriciinae, Dorvilleidae, Syllidae), (reviewed by Giangrande 1997). Greater dispersal ability is associated with planktonic larvae and although larval survival may be low during the pelagic phase, the greater numbers of offspring produced by *P. jouinae* sp. nov. compared to other interstitial polychaetes help explain its relatively high abundance in sandy sediment communities. In support of this the next most abundant species often found to co-occur with *P. jouinae* sp. nov. is the free spawning bivalve *Spisula solidissima* (Dillwyn, 1817). Other relatively less abundant co-occurring species include representatives of brooding interstitial polychaetes such as Dorvilleidae, Syllidae, and some members of the Hesionidae and Protodrilidae.

Changes in sediment composition and concomitant increases in organic loading affect the abundance and distribution of *Polygordius jouinae* sp. nov. thus making it a possible indicator of changing environmental conditions. A good example comes from the Rhode Island Region, long-term, dredged material disposal site (Battelle 2003). Prior to disposal of dredged material (primarily made up of muddy estuarine sediments), *P. jouinae* sp. nov. was the most abundant macrofaunal species at sites in the Rhode Island Sound Region (fall 2001). Following mud disposal (July 2003), *P. jouinae* sp. nov. no longer numbered among the top 10 species, and was replaced by the deposit feeding bivalve *Nucula annulata*. During this same time period the proportion of mud (<0.063 mm) in sediments increased from 7 % to 30 % (Battelle 2004).

## CONCLUSIONS

The present study was motivated by frequent reports in ecological studies conducted along the northeast USA of a highly abundant, and often dominant undescribed species of *Polygordius*. With this description, the range of *Polygordius jouinae* sp. nov. is presently known to lie between 39° N and 42° N. The species appears to thrive in sandy habitats in harbors, bays, and on the continental shelf to a maximum depth of 152 m on Georges Bank. It is the first North American *Polygordius* species to be described and is distinguished from most other *Polygordius* species by its non-bulging, heavily ciliated pygidium, absence of pygidial glands, and the conical (rather than rounded) prostomium. Morphologically similar species include *Polygordius triestinus* Hempelmann 1906 from the North Adriatic Sea, and *Polygordius triestinus* sensu Jouin (1970) from New Caledonia. *Polygordius jouinae* sp. nov. is distinguished from the former by being gonochoristic, and from the latter by not having pygidial glands. The 18S SSU rDNA from *P. jouinae* sp. nov. was sequenced and represents the first named *Polygordius* species with a DNA reference in GenBank (Accession number DQ153064). Spearman rank correlation of sediment grain size with density of *Polygordius jouinae* sp. nov showed that density was significantly ( $p = <0.05$ ;  $n=92$ ) positively correlated with the proportion of medium to very coarse sand and negatively correlated with the fine sand fractions. Given its widespread distribution along the east coast and its fidelity for coarse sand habitats its relative abundance may be useful as an indicator of changing sedimentary conditions.

Table 4.1: Synoptic table of characters of *Polygordius jouinae* sp. nov. with morphologically most similar species of the genus (all based on fixed specimens). Morphological information for *P. triestinus* and *P. triestinus* sensu Jouin (1970) from original species descriptions because type material was either lost or never deposited. Information for *P. antarcticus* taken from description and confirmed on paratype since holotype was not available. Character information based on observations of sexually mature individuals with the exception of *P. antarcticus*, and population measurements for *P. jouinae* sp. nov., which included some immature individuals. N/A indicates not applicable, n.d. indicates no data available, *n*=number of specimens measured, and F denotes observations taken from a figure rather than being explicitly stated in the text.

Character/ Species	<i>P. jouinae</i> sp. nov.	<i>P. triestinus</i> Hempelmann, 1906	<i>P. triestinus</i> sensu Jouin (1970)	<i>P. antarcticus</i> Rota and Carchini, 1999
Prostomium shape	conical	conical	conical	conical
Antenna length (mm)	Holotype (0.13) range (0.11-0.15; n=43)	n.d.	n.d.	0.075
Prostomium length (mm)	Holotype (0.14) range (0.11-0.15; n=43)	n.d.	n.d.	~0.15
Ratio (antenna: prostomium)	1:1	n.d.	n.d.	0.5:1
Antennae (close or spaced)	close	close	n.d.	close
Eyes	absent	absent	absent	absent
Pygidium shape	not inflated	not inflated	not inflated	inflated
Pygidial glands	absent	absent	present	present 28-30
Pygidial gland shape	N/A	N/A	n.d.	round
Pygidial cirri	absent	absent	absent	absent
Anal lobe (#)	7	n.d.	5 (F)	6-7
Body length (mm)	Holotype (19.4) Females (13.0-42.7; n=20) Males (13.8-43.1; n=23) population (3.0-23.5; n=318)	max 30	10-20	20 (subadult)
Body width (mm)	Holotype (0.23) Female (0.24-0.38; n=20) Males (0.23-0.34; n=23) population (0.06-0.32; n=318)	n.d.	n.d.	0.22-0.32 (subadult)
Segment (#)	Holotype (>65) Females (82-91; n=10)	n.d.	~60	82-98 (subadult)



Reproduction	Males (86-93; n=10 ) gonochoristic	hermaphrodite	only males found	n.d.
Type locality	NW Atlantic Ocean, United States, New Jersey, Tuckerton, Beach Haven Ridge	Northern Adriatic Sea, Italy, near Trieste	South Pacific Ocean, Bay of Saint- Vincent, New Caledonia	Antarctic Ocean, Ross Sea, Terra Nova Bay
Sediment type	medium to very coarse sand	muddy, oxygen poor sediments in relatively quiescent environments	medium sand with some fine material susceptible to variable salinities and strong currents	medium to coarse grained, well-oxygenated sands
Depth range (m)	5-152	n.d.	6-7	31-61

Table 4.2: Spearman's rank correlation between grain size and density of *Polygordius jouinae* sp. nov. (number m<sup>-2</sup>) at each subsite, Belmar, New Jersey over all sampling dates. Total  $n=92$ ;  $p<0.05$  (\*)  $p<0.01$  (\*\*)

Grain Size	mm	Spearman's Correlation	p-value
Pebble	>4	0.123	0.243
Granule	2-4	0.174	0.098
Very coarse	1-2	0.297**	0.004**
Coarse sand	0.5-1	0.314**	0.002**
Medium sand	0.25-0.5	0.265*	0.011*
Fine sand	0.125-0.25	-0.249*	0.019*
Very fine sand	0.062-0.125	-0.353**	0.001**
Mud	<0.062	-0.166	0.113

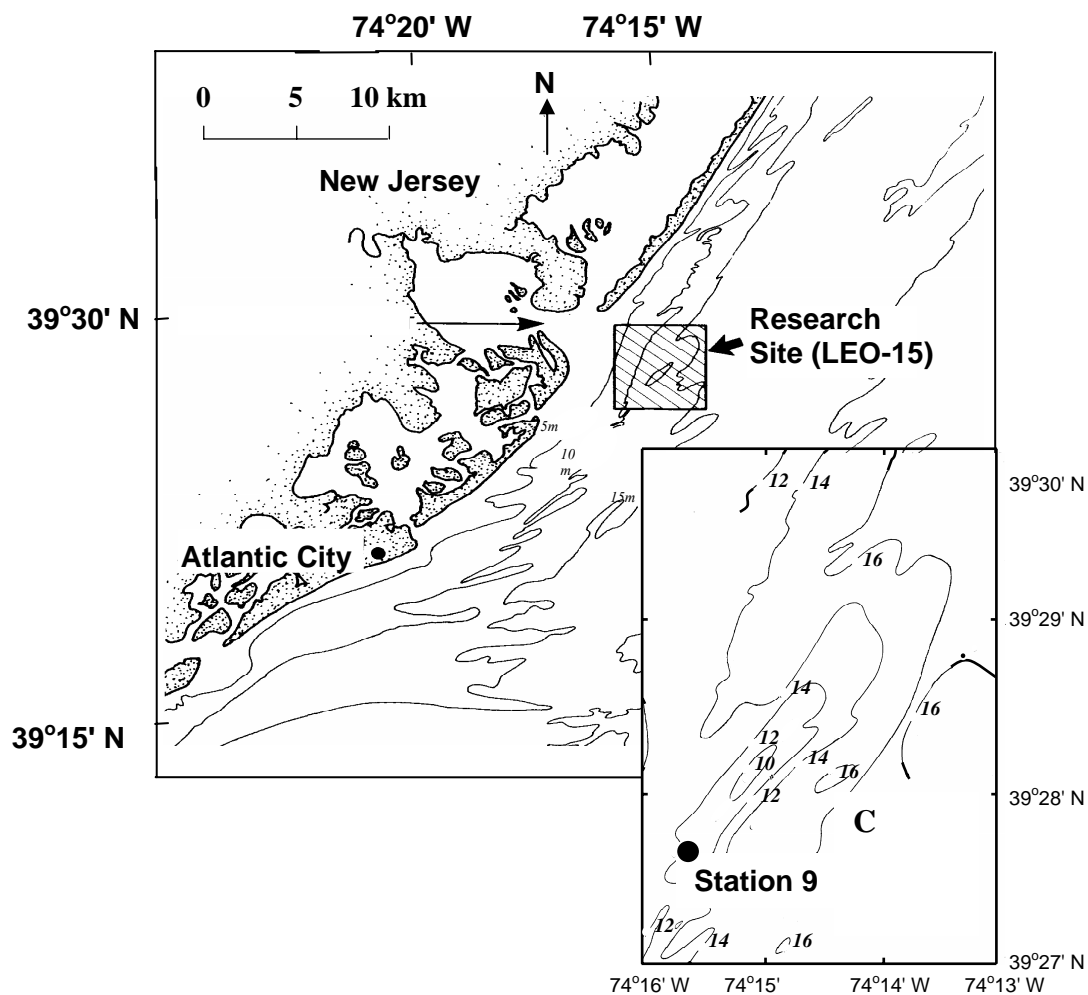


Fig.4.1. Map of research site LEO-15, continental shelf off New Jersey, USA. Smaller inset is of Beach Haven Ridge showing bathymetry (m) and type location, Sta. 9 of *Polygordius jouinae* sp. nov.

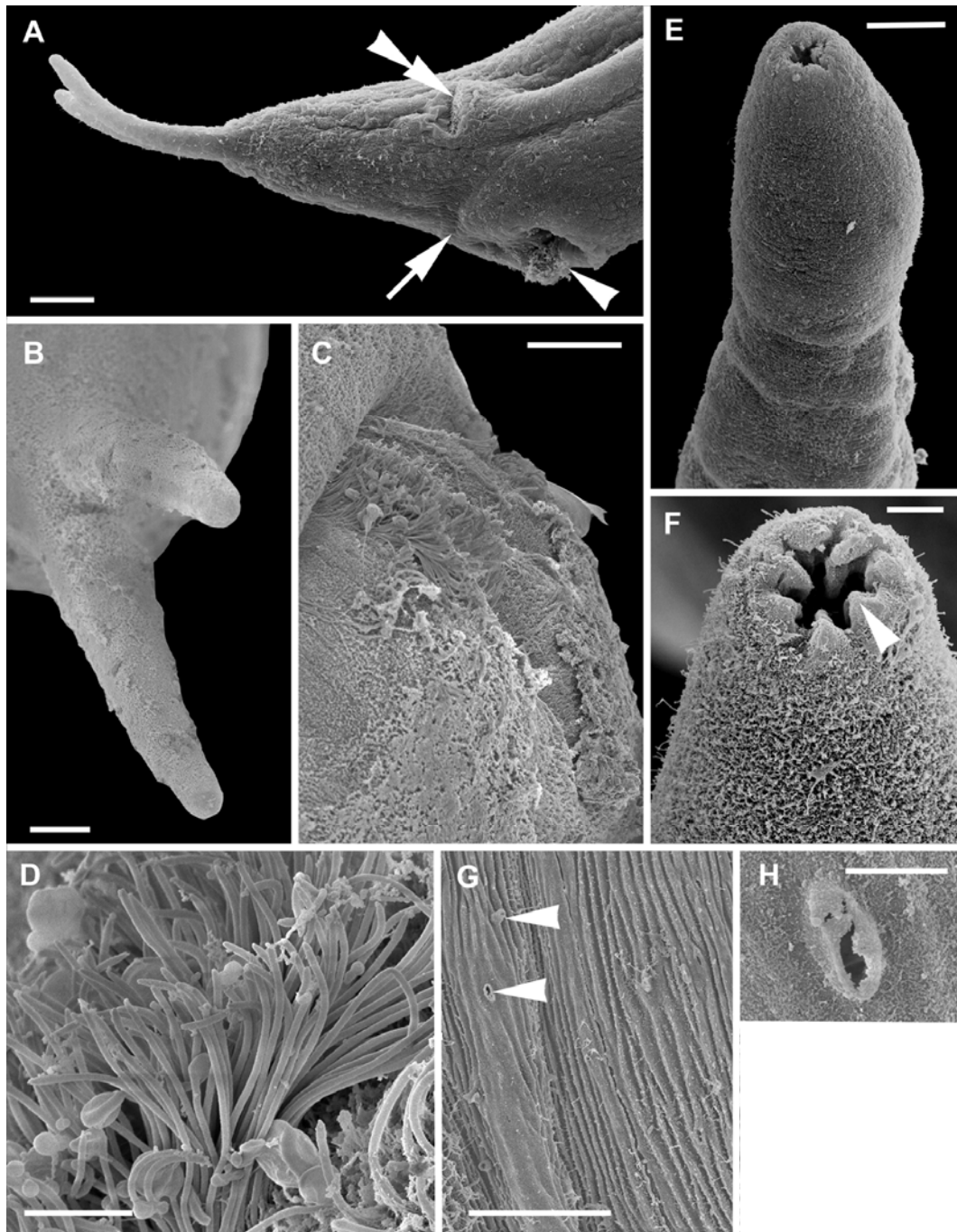


Fig. 4.2. Morphology of *Polygordius jouinae* sp. nov. (A) SEM showing a lateral view of conical prostomium, ciliated nuchal organ (double arrowhead), head fold demarcating the prostomium from the peristomium (arrow), and ventral mouth (arrowhead) (bar = 30- $\mu$ m). (B) SEM showing dorsal view of prostomium and paired antennae (bar = 12- $\mu$ m).

(C) High magnification of ventral mouth and ciliated buccal lip (bar = 10- $\mu$ m). (D) Higher magnification of cilia on buccal lip (bar = 2.5- $\mu$ m). (E) SEM showing lateral view of posterior end (bar = 30- $\mu$ m). (F) SEM showing lateral view of pygidium and seven anal lobes (arrowhead) (bar = 10- $\mu$ m). (G) SEM showing cuticular striations and body pores (arrowheads) (bar = 10- $\mu$ m). (H) High magnification SEM of body pore (bar = 1- $\mu$ m). Note: Fig. 4.2A, E, F are from a paratype SEM stub located at the SMF (SMF 15970 SEM stub No. 679), and Fig. 4.2 B, C, D, G, H are from a paratype SEM stub located at the YPM (YPM 38051). Figure modified from Ramey et al. (2006).

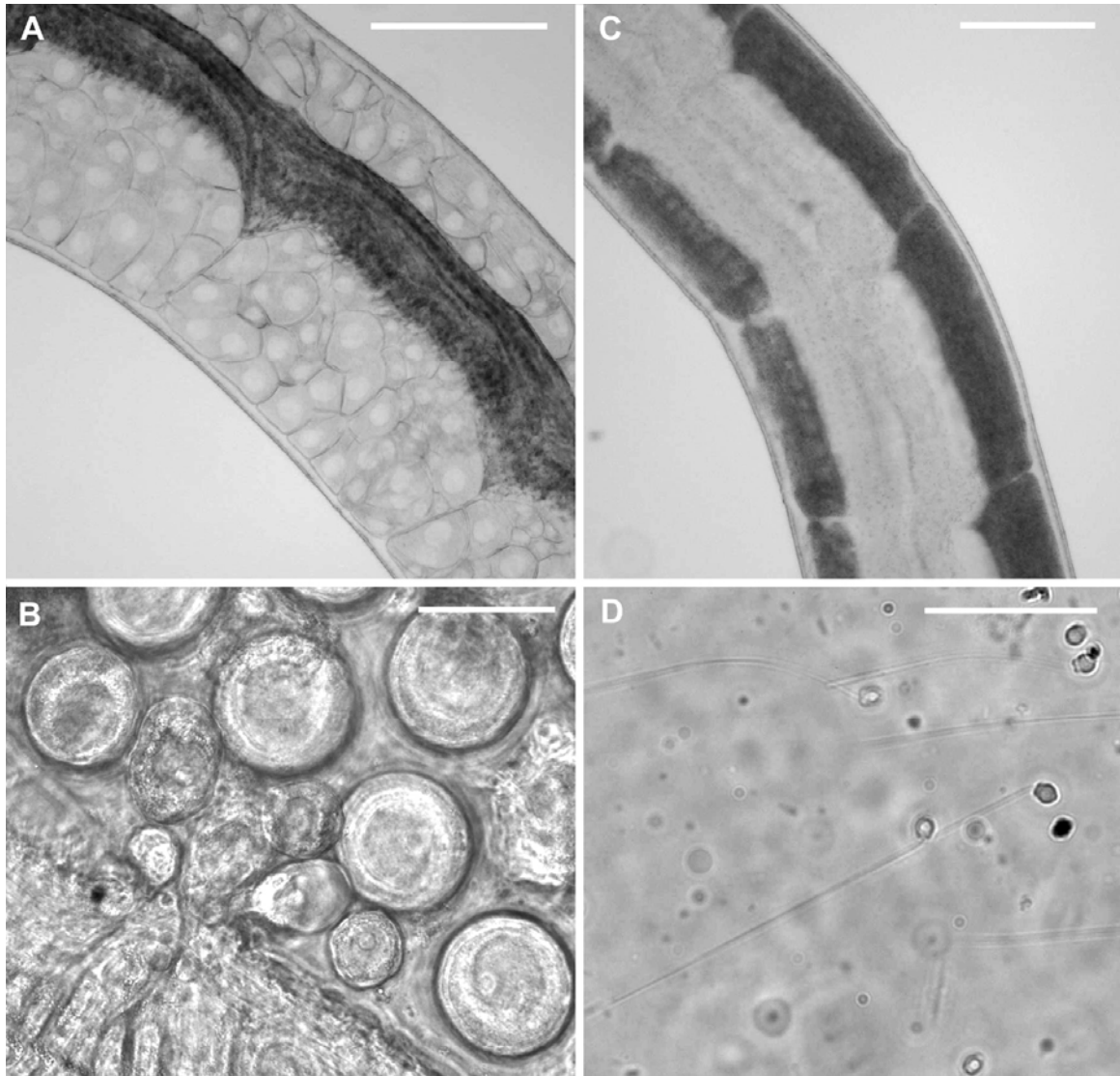


Fig. 4.3. Light micrographs of live mounted *Polygordius jouinae* sp. nov. (A) Female with oocytes tightly packed within coelom (bar = 190- $\mu$ m). (B) Oocytes bursting through body wall to surrounding medium (bar = 45- $\mu$ m). (C) Male with sperm packed within coelom (bar = 135- $\mu$ m). (D) Morphology of spermatozoa (bar = 25- $\mu$ m).

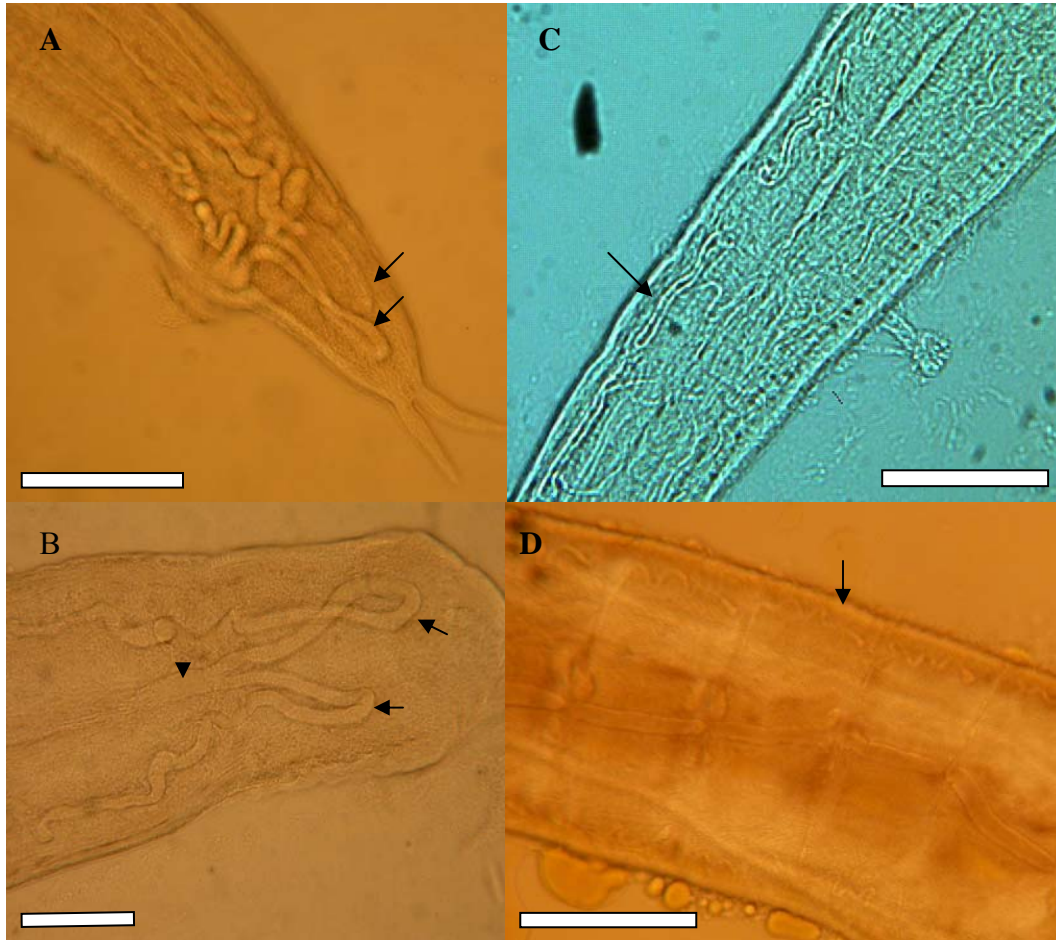


Fig. 4.4. Light micrographs of fresh mounted *Polygordius jouinae* sp. nov. showing part of the circulatory system. (A) Dorsolateral view of anterior portion of *P. jouinae* showing lateral loops or circumoesophageal blood commissures (arrow) (bar = 130- $\mu$ m). (B) Dorsal view of anterior portion of *P. jouinae* showing lateral loops or circumoesophageal blood commissures (arrow), dorsal blood vessel (arrowhead) (bar = 65- $\mu$ m). (C) Dorsal view of anterior foremost segments showing ventrolateral intersegmental blood commissures forming long loops (arrow) (bar = 130- $\mu$ m). (D) Dorsal view showing smaller blood vessels penetrating genital segments (arrow) (bar = 180- $\mu$ m).

## CHAPTER 5

### **LIFE HISTORY OF A DOMINANT POLYCHAETE, *POLYGORDIUS JOUINAE*, IN INNER CONTINENTAL SHELF SANDS OF THE MID-ATLANTIC BIGHT, USA**

#### INTRODUCTION

Although highly variable in space and time, marine soft-sediment macrofaunal communities demonstrate persistent patterns in community composition and abundance at various scales. Species with diverse life histories such as polychaetes have various mechanisms for dispersal and selection of new and existing habitats (Rouse and Pleijel 2001), and several studies have focused on larval dispersal and habitat selection as the primary factors responsible for observed population and community patterns (reviews by Scheltema 1986; Butman 1987; Underwood and Fairweather 1989). However, differences in species' life histories such as reproductive strategy, main reproductive period, total reproductive period, fecundity, type of development, average number of generations in a population, and life span also create and maintain observed temporal and spatial patterns of macrofauna (e.g., Zajac 1991; Kelaher and Rouse 2003; Hernández-Alcántara and Solís-Weiss 2005). Species' life history information is often absent in community level studies because the natural history of many macrofaunal species is unknown, especially for polychaetes, which make up the largest portion of soft-sediment infaunal abundance. Of 15,000 described species of polychaetes the complete life history is known for only ~3.0% of them (Giangrande 1997).

Benthic macrofaunal communities on the inshore continental shelf off Tuckerton, New Jersey have been the focus of several studies since the late 1970's (e.g., Boesch



1979; Garlo et al. 1979; Snelgrove et al. 1999, 2001; Grassle et al. 1999; Ma and Grassle 2004). Macrofauna important in determining local patterns at LEO-15 include oligochaetes, the polychaete *Mediomastus ambiseta* (Hartman 1947), and the bivalve *Nucula annulata* Hampson, 1971 which dominate muddy sands, whereas coarse sandy sediments are dominated by the surf clam *Spisula solidissima* (Dillwyn 1817), and the recently described polychaete *Polygordius jouinae* Ramey, Fiege, and Leander 2006 (formerly referred to as *Polygordius* sp.) (Snelgrove et al. 1999, 2001). *Spisula solidissima* can be very abundant with densities as high as  $2.4 \times 10^5$  individuals  $m^{-2}$  (Weissberger and Grassle 2003), and *P. jouinae* has at times made up >50% of macrofaunal abundance with densities as high as 98,400 individuals  $m^{-2}$  (Snelgrove et al. 2001).

The role of larval selectivity in creating observed adult spatial patterns at LEO-15 was demonstrated by Snelgrove et al. (1999, 2001) through three, 3 to 5-d reciprocal sediment transplant experiments at a coarse sand, and a muddy-sand site. The focal species in this study was the economically important surf clam, *Spisula solidissima*, and larvae selected coarse sand typical of adult habitats over muddy-sand. Several other taxa also exhibited selectivity consistent with field distributions. Among these was *Polygordius jouinae* (referred to as *Polygordius* sp.) which had significantly higher density in coarse sand compared to muddy-sand treatments. But unlike *S. solidissima*, larvae of *P. jouinae* were not present in associated plankton samples and individuals in transplant trays were not measured to establish the life stage(s) present. The expected size range of new recruits of this polychaete is unknown.

Recent research has revealed that the dominance of *P. jouinae* in well-sorted, sandy sediment communities was not limited to LEO-15 but it had also been collected in bays and harbors from Massachusetts to southern New Jersey (Ramey et al. 2006). Although small in size, these abundant worms occupy the interstices of sandy sediments, are highly motile deposit feeders, and likely have a major impact on sediment biogeochemistry (Ramey, unpublished). These characters along with the paucity of information on their biology, makes them of interest.

The present study characterizes the benthic phase of the life cycle of *P. jouinae* in the LEO-15 research area on Beach Haven Ridge. Intensive seasonal sampling conducted at LEO-15 from February 2004 to November 2005 examined temporal patterns of abundance, and size frequency distributions. Observations were made on their reproductive mode, reproductive period, size at maturity, the number of generations in a population, and life span. Additionally, *P. jouinae* present in ambient sediments, and in three reciprocal 3 to 5-day sediment transplant experiments at sandy and muddy sites collected by Snelgrove et al. (1999; 2001) were measured and size frequency distributions were determined for the first time. Analysis of these data provides a larger set of values for *P. jouinae* and this, along with the experimental design, provides further insight into life history, habitat selection, and dispersal of *P. jouinae* not considered by Snelgrove et al. (1999; 2001).

## MATERIALS AND METHODS

### Study location and seasonal sampling scheme

Research was conducted at Beach Haven Ridge, station 9 of the LEO-15 research site, New Jersey (Von Alt and Grassle 1992). Beach Haven Ridge (5 km long by 1.5 km wide) is one of 71 shore oblique, sand ridges on the continental shelf off New Jersey (McBride and Moslow 1991) and station 9 is located on the shoreward side of the ridge at ~ 12-m depth (39° 27.69' N, 74° 15.81' W). It was chosen because it has a coarse sand bottom (~0.50 mm grain size) where *Polygordius jouinae* is known to be abundant (Snelgrove et al. 1999; 2001). Seasonal sampling of *Polygordius jouinae* was conducted from February 2004 to November 2005. Samples were collected by SCUBA divers using hand held sediment corers (surface area 38.5 cm<sup>2</sup>, 7.0 cm diameter, 10 cm deep) with the exception of samples collected in February and March 2004 using a Van Veen grab (0.04 m<sup>2</sup>). In 2004, sediment cores were taken biweekly from April through December with a few exceptions (one sampling date in May, October, and December), (Table 5.1). In 2005, no cores were collected during April, October, and December due to weather, and biweekly samples were only collected for the critical months of May, June, and August (Table 5.1). For the majority of sampling dates at least six replicate cores were haphazardly collected ~1.8 m apart (Table 5.1).

### Sample treatment

Polychaetes become opaque after fixation, and therefore sediment samples were promptly sorted for *Polygordius jouinae* prior to fixation by placing small amounts of sediment and seawater in a tray with a white bottom. Using a dissecting microscope

individuals were classified as sexually immature or sexually mature males or females following Ramey et al. (2006). The remaining sediment sample, and a haphazardly determined subset of the live *P. jouinae* (some were kept alive for experimental and observational purposes) were transferred to 4% buffered formaldehyde, and subsequently transferred to 80% ethanol with rose bengal. Fixed sediment samples were processed over a 40- $\mu$ m sieve and re-sorted under a dissecting microscope to obtain any *P. jouinae* which may have been missed during the initial live sorting. On several dates (i.e. 6 October, 16 December 2004; 6 June, 12 July, and 21 September 2005) samples were not live sorted prior to fixation. Size was measured as total length (Ramey et al. 2006) and volume (Self and Jumars 1978). Measurements were performed on fixed material. Total length was measured from the anterior margin of the prostomium (antennae not included) to the posterior margin of the pygidium containing the anus. The width was taken at approximately the widest segment in the middle region of the body (Ramey et al. 2006).

#### Reciprocal sediment tray experiments and ambient faunal cores

In a previously conducted field experiment (with which new analyses and comparisons are made in the present study), ambient sediment cores were randomly collected by divers from ripple crests and troughs at LEO-15 station 9 once during July, September, and November 1994 ( $n=54$ ) and June 1995 ( $n=18$ ). Samples were fixed as described above, and processed over a 300- $\mu$ m sieve (see Table 5.1). Surface sediment (top 2-3 cm) for reciprocal treatment tray experiments was collected with a 0.04 m<sup>2</sup> Van Veen grab from LEO-15 coarse sand (station 9, 0.5 mm grain size Craghan 1995), and muddy-sand (station 32; 0.074 mm, grain size Craghan 1995), hereafter the “sandy” and

“muddy” stations respectively. It was then frozen, washed, sieved (1-mm mesh), and placed in hydrodynamically unbiased trays (described by Snelgrove et al. 1993). Due to the tray design worms can not enter the trays by migrating through the sediment. Therefore worms in trays had to either settle as larvae or juveniles had to be transported in from surrounding sediments. At both sites, three replicates each of sand and mud treatments were haphazardly interspersed at distances of several meters, at the same depth, along a line perpendicular to the predominant tidal flow and flush with surrounding sediments in ripple troughs. Sediment trays were left in situ for 3 to 5 days twice during August, and once in September 1994, and for 7 days on a single date in July 1995 (during a storm) (Table 5.1). Following retrieval, sediment trays were processed over a 100- $\mu\text{m}$  sieve and fixed. During the 1-4 August experiment two sand treatment trays were not recovered at the muddy site (see Snelgrove et al. [1999] for further details). In the present study, all intact *Polygordius jouinae* recovered from sediment treatment trays (1994) were measured, and a haphazard sample of 100 individuals was measured from ambient cores (3-7 cores sample date<sup>-1</sup>). Haphazard sampling of *P. jouinae* recovered from the 1995 sediment treatment trays (16-27 July,  $n=68$  ind) and ambient sediments (June,  $n=57$ ) were also measured.

#### Data analysis

Seasonal patterns of abundance for 2004 and 2005 were examined by producing smoothing curves based on running averages of *Polygordius jouinae* abundance (number individuals 100 cm<sup>-2</sup>) plotted against sampling date (Julian day) using the graphing software Sigma plot 8.0. Size-frequency distributions of *P. jouinae* for each sampling date

were produced for the seasonal (2004 and 2005), treatment tray (1994 and 1995), and ambient sediment (1994 and 1995) data. Size frequency distributions based on total length and volume produced similar results, so frequency distributions based on total length are presented. Total length measures combined with live observations as to whether individuals were sexually mature indicated that sexually mature individuals were 13 to 43 mm in total length (Ramey et al. 2006). Pulses of smaller immature *P. jouinae* present following the appearance of sexually mature individuals were usually  $\leq 9$  mm in total length and were designated as juveniles. Given this, immature individuals 10 to 12 mm in total length were considered as adults. Thus, size categories for frequency distributions were expressed in multiples of three with individuals measuring  $\leq 9$  mm classified as juveniles, and adults were  $>9$  mm. Length frequency distributions for treatment trays included total length measures of *P. jouinae* recovered from both sand and mud treatments. Differences in mean total length among dates were tested for those dates having  $n > 12$  individuals using a non-parametric Mann-Whitney U test ( $\alpha = 0.05$ ) in SPSS 10. The percentage of total individuals that were sexually mature was calculated for live-sorted samples only. Mean total length of *P. jouinae* and SD was compared in each replicate for reciprocal tray experiments. Differences in total length among dates were determined using a Kruskal-Wallis test performed in SPSS 10.

## RESULTS

Density of *Polygordius jouinae* was low during the winter and early spring of 2004 (i.e. sampling dates in February, March, and April,  $\bar{x} = 13$  ind 100 cm<sup>-2</sup>) and peaked on the May sampling date ( $\bar{x} = 311$  ind 100 cm<sup>-2</sup>) (Fig. 5.1A). Within 12 days, from 27

May to 7 June, density decreased by half (7 June:  $\bar{x}=159$  ind 100 cm<sup>-2</sup>) and continued to decline throughout the summer (i.e. sampling dates from July to September) (Fig. 5.1A). Density remained low during the fall and winter 2004/2005 (i.e. sampling dates from October to March) (Fig. 5.1A, B). Although abundance of *P. jouinae* was much lower in 2005 compared to 2004, patterns of abundance during the first part of the year were similar, with low density in the winter (i.e. sampling dates in February and March,  $\bar{x}=6$  ind 100 cm<sup>-2</sup>), higher in May ( $\bar{x}=21$  ind 100 cm<sup>-2</sup>) and lower levels in June ( $\bar{x}=2$  ind 100 cm<sup>-2</sup>). However unlike the previous year, density was higher on the July sampling date and a peak in yearly abundance was observed in early August ( $\bar{x}=55$  ind 100 cm<sup>-2</sup>) (Fig. 5.1B). During both years sexually mature individuals, with a sex ratio of ~1:1 (males:females), were first observed in May followed by recruitment of juveniles (TL  $\leq 9$  mm) in July (Fig. 5.1A, B and Fig. 5.2A, B).

Size frequency distributions of *Polygordius jouinae* for 2004 showed that individuals in June were significantly larger ( $\bar{x}$  TL=19.75 mm) than those collected in the winter and early spring (i.e. February/March/April,  $\bar{x}$  TL=13.55 mm), as well as those collected throughout the summer and fall (July, August, October, December), ( $p<0.05$ , Fig. 5.2A). In June 2004, all individuals were sexually mature and at the end of July sexually mature individuals formed 79% of the total number (Fig. 5.2A). Worm length increased on sampling dates from July to October but differences were not significant ( $p>0.05$ , Fig. 5.2A). Length frequency distributions for 2005 showed that individuals sampled in May were significantly larger ( $\bar{x}$  TL=25.8 mm) than those in mid-July ( $\bar{x}$  TL=7.28 mm), and on two dates in August (i.e., 9 August  $\bar{x}$  TL=9.16 mm,

17 August ( $\bar{x}$  TL=9.62 mm) ( $p<0.05$ , Fig. 5.2B). In 2005, the mid-July sampling marked the first appearance of juvenile size classes (TL  $\leq$  9 mm), following the appearance of sexually mature individuals which were significantly smaller than those sampled on the two dates in August, ( $p<0.05$ , Fig. 5.2B). Total worm length was not significantly different between the two August sampling dates ( $p>0.05$ ) (Fig. 5.2B). Individuals in May were all sexually mature and by early and mid-August the percentage of sexually mature individuals was reduced to 34% and 26% respectively (Fig. 5.2B). The mean total length of individuals for July and August 2005 ( $\bar{x}$  TL=8.96 mm) was significantly less than observed in 2004 for the same months ( $\bar{x}$  TL= 12.36 mm) (Fig. 5.2A, B).

Comparisons of total lengths for *P. jouinae* in sediment treatment trays indicated significant differences in size distribution with date (Kruskal-Wallis chi-square=83.24,  $P<0.001$ , total=365) (Fig. 5.3). Specifically, total length was significantly greater in September ( $\bar{x}$  TL= 6.10 mm) compared with the two dates in early and mid-August ( $\bar{x}$  TL= 4.15 mm and 4.00 mm, respectively) ( $p<0.05$ , Fig. 5.4A), but no significant difference was found when the two August dates were compared ( $p>0.05$ , Fig. 5.4A). Sediment treatment trays contained almost 100% juvenile *P. jouinae* (TL  $\leq$  9 mm) (Fig. 4A). The total length of *P. jouinae* in ambient sediments differed significantly among all three dates ( $p<0.05$ ), with larger individuals observed in July ( $\bar{x}$  TL= 16.03 mm), and the smallest individuals in September ( $\bar{x}$  TL= 6.03 mm) (Fig. 5.4B).

## DISCUSSION

Understanding species' life histories and reproductive biology is critical to fully understanding the structure and dynamics of populations and communities. This study



characterized the benthic phase of the life cycle of the first member of the family Polygordiidae, *Polygordius jouinae*, to be described from North America. This small, interstitial polychaete is a dominant member of macrofaunal communities in coarse sands on the continental shelf and in bays and harbors of the Mid-Atlantic Bight (Ramey et al. 2006). *Polygordius jouinae* is gonochoristic, shows no signs of sexual dimorphism, and the ratio of sexually mature males to females is ~1:1. The reproductive period generally occurs from May to August and individuals appear to have a 1 year life span. In late May 2004 and 2005 the population was comprised of sexually mature individuals and by June abundance declined with a corresponding loss of larger sexually mature individuals from the population. Similarly in 1994, larger individuals found in ambient sediments in July were no longer present by mid-September. Eggs (<62- $\mu$ m) and sperm are believed to be set free through rupture of the body wall (Ramey et al. 2006) and individuals are thought to die after spawning. Recruitment begins no later than July as recently settled individuals (< 9 mm body length) which were not present during the first week of June 1995, 2004, and 2005, first appeared in July in all three years. Although a few individuals in the 9-mm category were present for the combined months of February, March and April 2004 ( $n=3$ ; one individual per month) no sexually mature individuals were observed during this time, and here individuals likely represent late recruits and/or slow growing individuals from the previous summer. The smallest individual recorded was 2.01 mm total length and this provides the first estimate of size at initial recruitment. In the North Sea near Helgoland, Nordheim (1984) studied the life history of several interstitial polychaetes including *Polygordius appendiculatus* Fraipont, 1887 and *Polygordius*

*lacteus* Schneider, 1868. Life cycle and life history traits for these two species are summarized and compared with *P. jouinae* in Table 5.2.

In the present study, year-to-year variation in population abundance and recruitment of *P. jouinae* was observed. In spite of sexually mature individuals being 30 times more abundant in May 2004 compared to 2005, recruitment in 2004 was much lower and no substantial peak in recruitment was observed. The continual decline in abundance observed from May to September 2004 was not found in 2005. Instead abundance declined from the end of May to June. It is possible that a large portion of the 2004 population never spawned. By the end of July 2004, 79% of the population was still sexually mature compared to 34% in early August 2005 and larger individuals present in June 2004 were present throughout the summer (i.e. June to September) along with a very low abundance of recently settled juveniles. In contrast, only the smallest individuals present in May 2005 were still found in June with a relatively higher abundance of recently settled individuals beginning in July. Moreover, over-wintering of non-spawning individuals present in the summer of 2004 could explain the relatively low abundance and skewed range of size frequencies present in the May 2005 samples which included some relatively large individuals (i.e. >30 mm). Observations on sexually mature *P. jouinae* collected in May and kept alive in static laboratory cultures for more than 6 months (with sediment at 15°C) indicated that they resorbed their gametes. Within a few weeks following their collection, spawning had not been observed (which should have resulted in death) and gametes were no longer visible. Thus, non-spawning individuals of *P. jouinae* could potentially live longer than one year and therefore the population may sometimes consist of individuals of two generations.

Common adaptations of interstitial polychaetes usually include low gamete production, direct development, large eggs, brooding, or formation of a cocoon. However, unlike other interstitial polychaetes (with the exception of Protodrilida) Polygordiidae develop via a planktotrophic larva which may be in the water column for several weeks (Rouse and Pleijel 2006) (Table 5.2). The relatively large numbers of small eggs (1000's maximum; diameter <62- $\mu$ m) and sperm structure in *P. jouinae* indicate free spawning with planktotrophic larvae (Ramey et al. 2006). Two planktonic larval forms have been described for *Polygordius* spp. including an exolarva, in which the larval body becomes gradually elongated by addition of new segments posterior to the hyposphere (Hatschek 1878), and an endolarva in which the developing segments remain folded up inside the trochophore until metamorphosis occurs, when large parts of the body are cast off (e.g., Lovén 1843; Woltereck 1902) (Table 5.2). Although larvae of *P. jouinae* were not sampled in the present study, studies as early as 1883 reported both types of *Polygordius* spp. larvae as abundant along the east coast of the United States, several decades before adult *Polygordius* sp. were reported. At Beaufort, North Carolina actively swimming endolarvae were collected in August (Cowles 1903). A single larva ~1 mm long, had metamorphosed by the next day (2 mm length) and grew rapidly to 15 mm in six weeks (Cowles 1903). *Polygordius* spp. larvae have also been reported within the known range for adult *P. jouinae*. Larvae of unknown type were observed in early summer (i.e. June/July) at Woods Hole, Massachusetts (Bumpus 1898) and exolarvae have been found off Newport, Rhode Island (Fewkes 1883; Ritter 1892). Exolarvae were present in the water column several weeks before and after 9 August 1890 and in the lab they grew quickly, although no measurements were taken (Ritter 1892). Although not

explicitly stated, figures of the exolarvae from Rhode Island do not include anal cirri. It is possible that the exolarvae collected off Rhode Island belong to *P. jouinae* as Stickney and Stringer (1957) noted the presence of a new species of *Polygordius* in well sorted sand communities of Greenwich Bay, Rhode Island. The posterior end of this *Polygordius* species, like *P. jouinae* is not inflated (lacks a caudal enlargement) (Ramey et al. 2006). Moreover, numerous *Polygordius* sp. specimens collected from sandy sediments in Rhode Island Sound, in July 2003 were identified as *P. jouinae* (Ramey et al. 2006).

*Polygordius jouinae* appears to thrive in coarse sandy sediments, and at Belmar, New Jersey, density of *P. jouinae* has been shown to be significantly positively correlated with the proportion of medium to very coarse sand and negatively correlated with fine sand (Ramey et al. 2006). Density of this species was significantly higher in sandy, than in muddy treatments in the 3 to 5-day reciprocal transplant experiments of Snelgrove et al. (1999). The present study shows that *P. jouinae*  $\leq 3$  mm in length found in sediment trays are of the expected size range for very recent settlers. However, most worms in treatment trays were recently settled juveniles (length categories 6 and 9-mm) transported in from surrounding sediments, presumably as a consequence of re-suspension or bedload transport. As expected, larger individuals were present later in the summer. Although it is unknown whether *P. jouinae* were transported actively or passively, these data suggest that recently settled juveniles as well as larvae are capable of habitat selection, emphasizing the importance of post-settlement transport and selection in influencing community structure. Several authors have noted that species living in such hydrodynamically/disturbed habitats tend to disperse more than species living in stable

habitats (e.g., Palmer et al. 1996). Thus both larval and post-settlement transport may be important for macrofauna inhabiting permeable, sandy sediments on the continental shelf which are frequently eroded by tides, waves, and storms, transported horizontally, and deposited (e.g., Styles and Glenn 2000). Of the 15 species and two subspecies described in the genus *Polygordius* Schneider, 1868, all but one have been found in intertidal or subtidal coarse sandy sediments.

## CONCLUSIONS

*Polygordius jouinae* is gonochoristic and the ratio of sexually mature males to females is ~1:1. The population was mostly composed of sexually mature individuals in late May 2004 and 2005. The reproductive period generally occurs from May to August and spawning individuals generally have a one year life span. Recruitment begins no later than July as recently settled individuals ( $\leq 9$  mm body length) which were not present during the first week of June 1995, 2004, and 2005, first appeared in July in all three years. The smallest individual was 2.01 mm long and this provides the first estimate of size at initial recruitment. Although some worms in sediment trays likely settled as larvae, most worms were recently settled juveniles (length categories 6 and 9 mm) transported in from surrounding sediments, presumably as a consequence of re-suspension or bedload transport. As expected, larger individuals were present later in September. Although it is unknown whether *P. jouinae* were transported actively or passively these data suggest that recently settled juveniles are capable of habitat selection (preferred sand over mud) and show that post-settlement transport and selection influence community structure. *P. jouinae* and Polygordiidae in general appear to be well adapted

for interstitial life in physically active, highly disturbed areas with coarse sandy sediments. A combination of life history traits such as high numbers of planktotrophic larvae, rapid development and growth of larvae and recruits, along with their dispersal ability and habitat selection, likely contribute to their widespread distribution and community dominance.

Table 5.1: Date and station (Sta. 9=sandy, Sta. 32=muddy), habitat type (i.e., C=ripple crest, T=ripple trough, s=sand, m=mud), number of samples, samp.gear (sampling gear [c=hand corer 38.5 cm<sup>2</sup>, t= sediment tray 100 cm<sup>2</sup>, vv= Van Veen grab 0.04 m<sup>2</sup>]), and sieve (µm) (mesh size for benthic samples).

Date and station		Number of samples	Samp. gear	Sieve (µm)
<b>1994/95 Ambient st. 9</b>				
20 Jul 94		18 (9 C, 9 T)	c	300
20 Sep 94		18 (9 C, 9 T)	c	300
14 Nov 94		18 (9 C, 9 T)	c	300
5 Jun 95		18 (9 C, 9 T)	c	300
<b>1994/95 Experimental trays</b>				
1-4 Aug 94	St. 9	3 s, 3 m	t	100
	St. 32	1 s, 3 m		
16-19 Aug 94	St. 9	3 s, 3 m	t	100
	St. 32	3 s, 3 m		
14-19 Sep 94	St. 9	3 s, 3 m	t	100
	St. 32	3 s, 3 m		
16-27 Jul 95	St 9	3 s, 3 m	t	100
	St 32	3 s, 3 m		
<b>2004 Seasonal st. 9</b>		total n=95		
26 Feb		3	vv	100
23 Mar		3	vv	100
9 Apr, 26 Apr		6, 6	c	40
27 May		6	c	40
8 Jun, 16 Jun		6, 6	c	40
2 Jul, 14 Jul, 30 Jul		5, 5, 5	c	40
9 Aug, 26 Aug		6, 6	c	40
13 Sep, 22 Sep		5, 6	c	40
6 Oct		4	c	40
2 Nov, 23 Nov		5, 6	c	40
16 Dec		6	c	40
<b>2005 Seasonal st. 9</b>		Total n=83		
9 Feb		6	c	40
22 Mar		6	c	40
19 May, 27 May		6, 10 (5 C, 5 T)	c	40
9 Jun		15 ( 3C, 12T)	c	40
12 Jul		6 (3 C, 3 T)	c	40
9 Aug, 17 Aug		6, 12 (6 C, 6 T)	c	40
21 Sep		8 (4 C, 4 T)	c	40
14 Nov		8	c	40

Table 5.2: Life cycle and life history traits of three species of *Polygordius*. Maximum length (mm), life span (year), number of generations in a population, reproductive mode= gon: gonochoristic (separate sexes), monotelic= mon (reproduces once a year) or polytelic= pol (reproduces several times a year), main reproductive season (months when >50% of the population is made up of sexually mature males and females), larval type=exo (exolarvae), endo (endolarvae), number of eggs per female, and sperm type= ect (ect-aquasperm-large numbers of small sperm released in broadcast spawning). Data for *Polygordius lacteus* and *Polygordius appendiculatus* from Nordheim (1984) unless otherwise specified with superscripts: f, h, j, r, and s for Fraipont (1887), Hempelmann (1906), Jamieson and Rouse (1989), Ramey et al. (2006), and Schneider (1868) respectively.

Life history traits	<i>P. jouinae</i> Ramey, Fiege, Leander 2006	<i>P. appendiculatus</i> Fraipont 1887	<i>P. lacteus</i> Schneider 1868
max length (mm)	45	20 <sup>f</sup>	100 <sup>h</sup> , 50 <sup>s</sup>
life span	1 y	10-15 mo	>1-2 y
# generations in population	1-2	≥2	1-2
reproductive mode	gon	gon	gon
monotelic or polytelic	mon	mon	pol
main reproductive season	May-Aug	end May-Oct	May-Sep
larval type	exo	endo	endo
# eggs female <sup>-1</sup>	several 1000 <sup>r</sup>	1500-2800	2000-3500
sperm type	ect <sup>f</sup>	n.d.	ect <sup>j</sup>
evidence of regeneration	no	no	yes



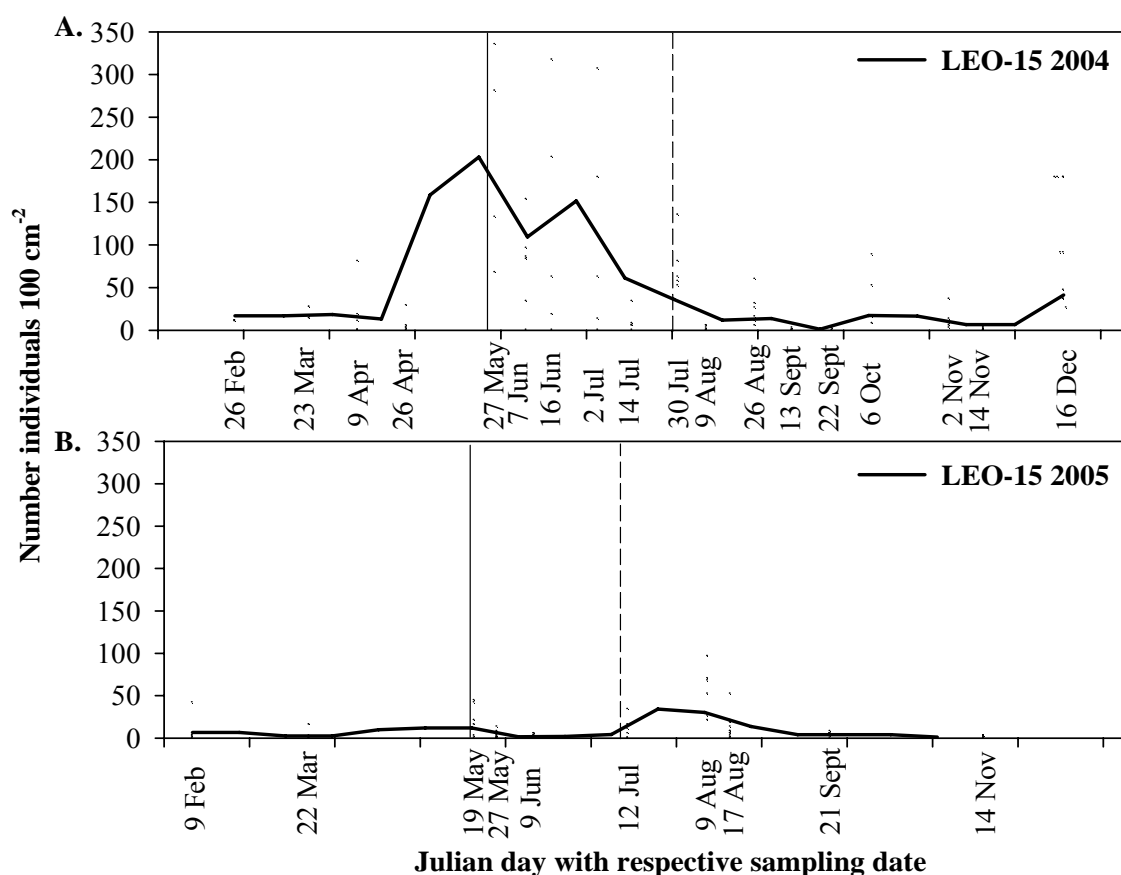


Fig. 5.1. *Polygordius jouinae*. Seasonal patterns in abundance (# ind 100 cm<sup>-2</sup>) at Sta. 9, LEO-15 plotted as Julian day (A) February to December 2004 (B) February to November 2005. Horizontal solid lines represent smoothing curves based on running averages (dots=raw data used to produce curve,  $n = 5$  to 15 replicate samples depending on date (see Table 6.1). Perpendicular solid lines indicate first appearance of sexually mature individuals; dashed lines indicate first recruits (defined as individuals  $\leq 9$  mm TL)

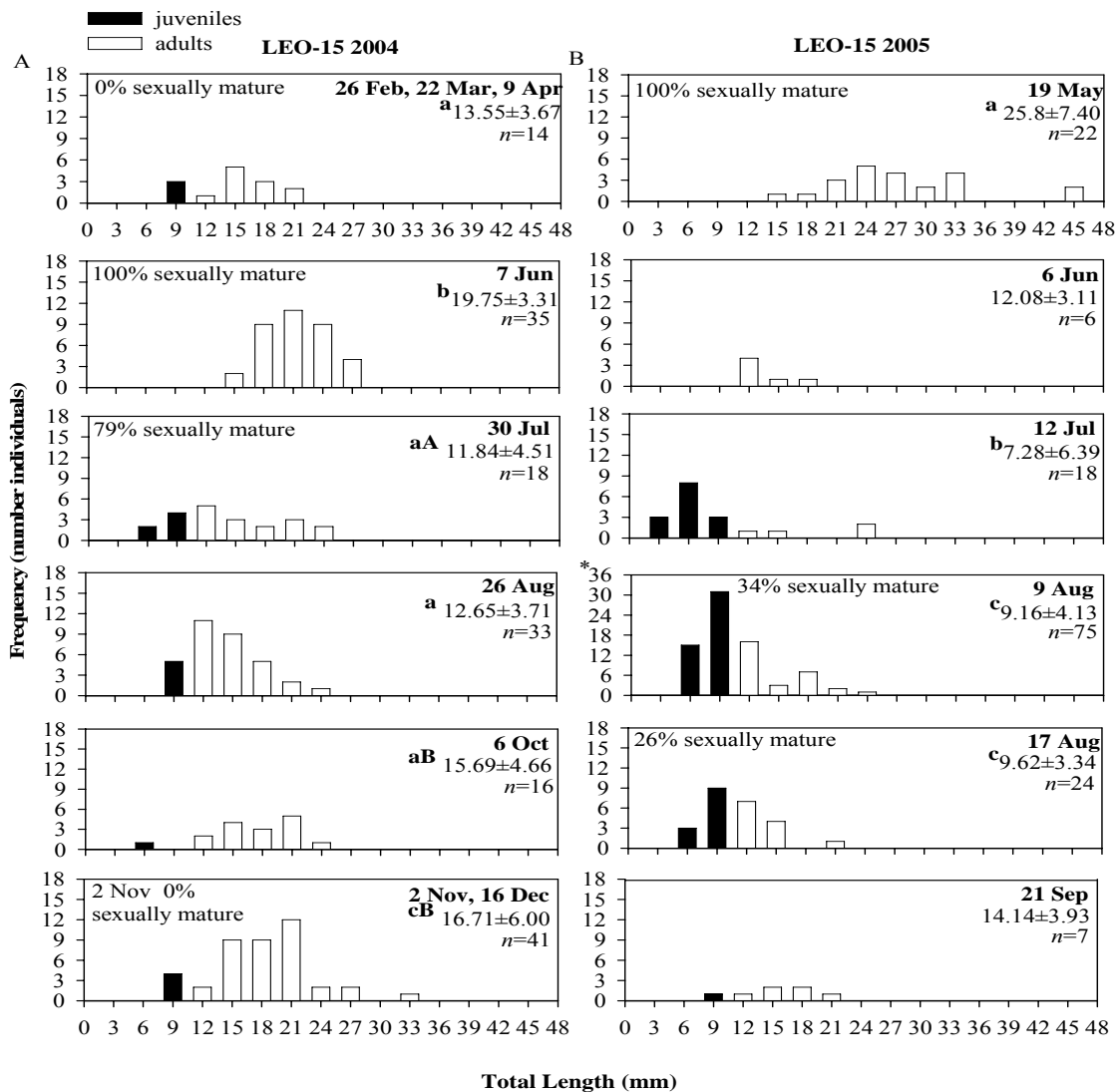


Fig. 5.2. *Polygordius jouinae*. Size frequency distribution with mean total length  $\pm$ SD for sampling February to December, 2004 and May to August, 2005. Size categories expressed in multiples of three (e.g., category 3= total length (mm)  $\leq 3$ , category 6= total length (mm)  $> 3 \leq 6$  etc.). Filled bars represent juveniles (defined as individuals  $\leq 9$  mm TL). Open bars represent adults ( $> 9$  mm TL). \*=scale on y axis differs. Percentage sexually mature refers to the proportion of sexually mature individuals out of the total collected and live sorted. (A) seasonal sampling 2004, dates with same letters (a, b, c or A, B) not significantly different ( $p > 0.05$ , Mann-Whitney U Test) (B) seasonal sampling

2005, dates with same letters (a, b, c) not significantly different ( $p > 0.05$ , Mann-Whitney U Test). Note: plots with multiple sampling represent pooled data

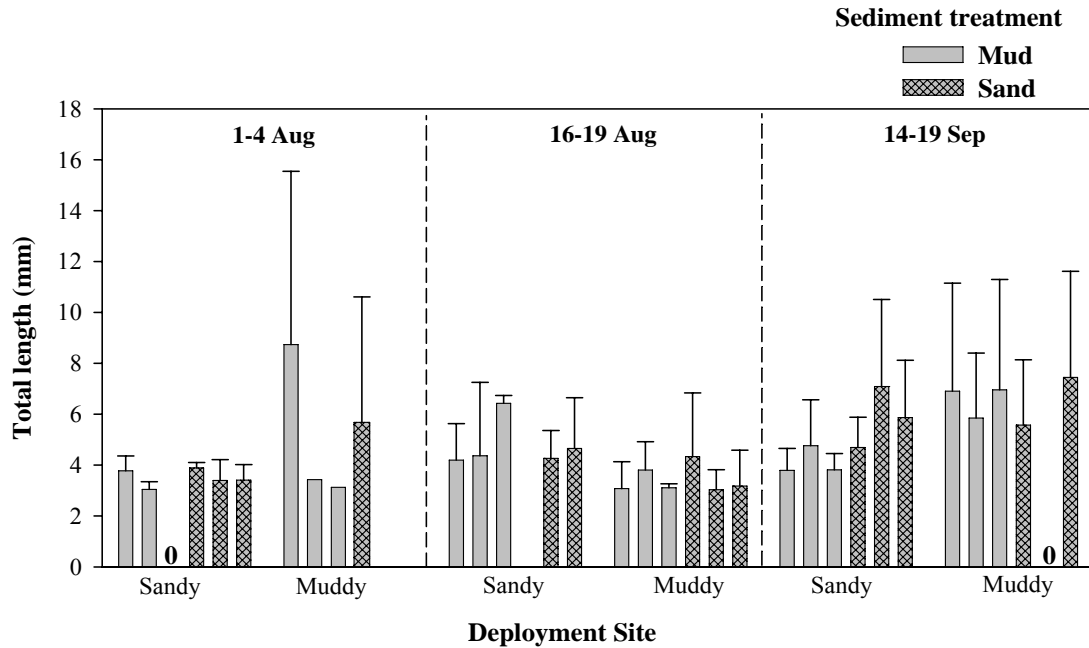


Fig. 5.3. *Polygordius jouinae*. Mean total length  $\pm$ SD in each replicate of reciprocal tray experiments (1994). Bar shading refers to sediment treatment. Densities in mud were low and means were usually based on  $<10$  individuals; means for sand based on  $>10$  but  $\leq 57$  individuals. Comparisons of total lengths indicated significant differences in size distribution with date (Kruskal-Wallis chi square=83.24,  $P<0.001$ ,  $n$  total=365). Sandy site=Sta.9 and muddy site=Sta. 30.

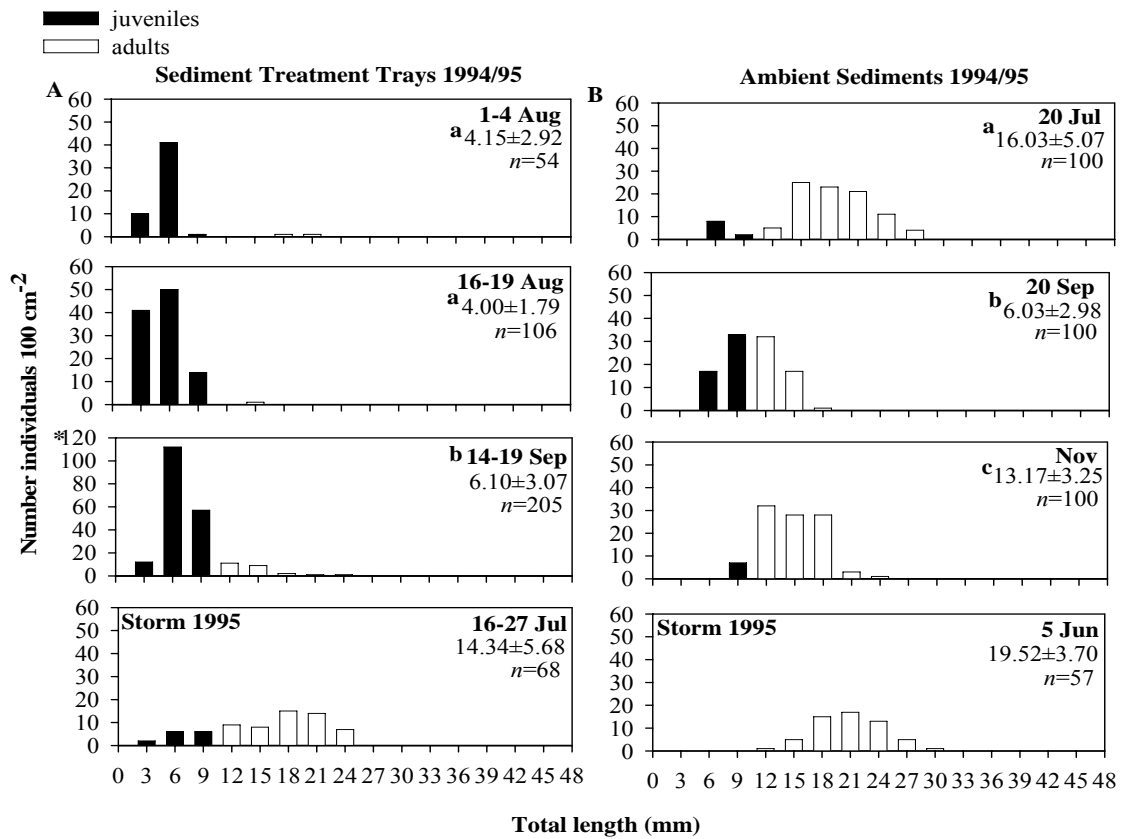


Fig. 5.4. *Polygordius jouinae*. Size frequency distribution with mean length  $\pm$ SD for ambient sediment and trays for each sampling period in 1994 and 1995 (storm). Size categories expressed in multiples of three (e.g., category 3= total length (mm)  $\leq 3$ , category 6= total length (mm)  $> 3 \leq 6$  etc.). Filled bars represent juveniles (defined as individuals  $\leq 9$  mm TL). Open bars represent adults ( $> 9$  mm TL) (A) sediment trays for 1-4 Aug 1994 ( $n= 54$  ind.), 16-19 Aug 1994 ( $n= 106$  ind.), 14-19 Sep 1994 ( $n= 205$  ind) and 27 Jul 1995 ( $n=68$  ind). Dates with same letters (a, b) not significantly different ( $p>0.05$ , Mann-Whitney U Test). (B) ambient sediments for 20 Jul 1994 ( $n=100$  ind), 20 Sep 1994 ( $n=100$  ind), Nov 1994 ( $n=100$  ind) and 5 June 1995 ( $n=57$  ind). Dates with same letters (a, b, c) not significantly different ( $p>0.05$ , Mann-Whitney test). \*=scale on y-axis differs.

## CHAPTER 6

### **SELECTION BY A DEPOSIT-FEEDING POLYCHAETE, POLYGORDIUS JOUINAE, FOR SEDIMENT ENRICHED WITH ORGANIC FLOCS**

#### INTRODUCTION

Sedimentary landscapes in high energy, physically active continental shelf environments encompass a rich array of habitats or patch structures which appear significant to benthic organisms (e.g., Hogue and Miller 1981; Able et al. 2003; Zajac et al. 2003; Barros et al. 2004). Small-scale patch dynamics and dispersal of infaunal organisms in these environments are poorly understood, even though such knowledge is critical to predicting ecological responses to long-term habitat changes on continental shelves. It is well established that infauna are patchily distributed on many spatial scales, and population and community patterns are created and maintained by complex interactions among a host of biological and environmental factors (reviewed by Ólafsson et al. 1994; Snelgrove and Butman 1994). Moreover, ecological patterns and processes operating at one spatial scale may differ from those at another scale (Dayton and Oliver 1980; Levin and Huggett 1990; Whitlatch et al. 1998) or in another environment. At larger spatial scales primary factors responsible for infaunal distribution patterns may include sediment grain size (Snelgrove and Butman 1994), larval dispersal, habitat selection (reviews by Scheltema 1986; Butman 1987; Underwood and Fairweather 1989), and predation (Wilson 1990; Ólafsson et al. 1994; Thrush 1999; Gallucci et al. 2005). At relatively smaller scales, dispersal and habitat selection by mobile, post-larval juvenile and adult stages seeking food may play a central role. Availability of food can stimulate

the migration of organisms to areas where food resources are more abundant (Hughes 1993; Nilsson et al. 2000) and information on the patchiness of species and resources is used in many ecological models and in generating ecological theory (Pickett and White 1985).

Sedimentary particulate organic matter (derived from organic rich flocs containing phytodetritus, decomposing macroalgae, fecal pellets, microorganisms, and to a lesser extent seagrass and land-derived detritus) is an important component of the diet of many infaunal organisms. Particulate organic matter concentrations decrease with increasing grain size of the sediment. Thus its relative abundance in the coarse, sandy sediments that cover ~70% of continental shelves (Emery 1968), may be especially important in influencing infaunal distribution patterns. Although poor in particulate organic matter, the high permeability of sandy sediments allows for concentrating mechanisms such as pore-water advection, a process not possible in finer sediments. This advection can enhance the levels of fresh particulate organic matter in the top several centimeters of the sediment (Eckman 1990; Pilditch et al. 1998). The main driving forces of advection are pressure gradients along the sediment surface. These develop whenever unidirectional or oscillating bottom flows are deflected by topography (Huettel and Gust 1992; Precht and Huettel 2003) and since current speed, direction, and topography on continental shelves, change on time scales from seconds to seasons, particulate organic matter is often distributed in a highly patchy manner at relatively small scales. Moreover, the interaction of flow with microtopography may also enhance deposition nearby (Eckman 1990; Yager et al. 1993; Pilditch et al. 1998) by creating regions of reduced shear stress (Pilditch and Miller 2006). Thus, heterogeneity generated by ubiquitous and

persistent microtopographic habitats such as ripples may be an important source of microhabitat specialization and resource partitioning (Hogue and Miller 1981).

Biogeochemical reactions within the sediment can also further influence patchiness in organic matter as well as the availability of oxygen, nutrients, and heavy metals (Ziebis et al. 1996; Huettel et al. 1998; Precht and Huettel 2004; Janssen et al. 2005).

Most infauna in sandy sediments are small, interstitial, relatively mobile species that are often patchily distributed horizontally at small scales (e.g., Eckman 1979), even when sediment grain size is homogeneous (e.g., Sandulli and Pinckney 1999). Studies have related spatial distribution of some infauna to food resources (Decho and Fleeger 1988; Santos et al. 1995) and the supply of particulate organic matter on continental shelves has been positively correlated with pulses of infaunal activity (Gerino et al. 1998; Stead and Thompson 2003). Infaunal distribution patterns have also been associated with microtopography (e.g., Hogue and Miller 1981; Kendrick et al. 1998; Barros et al. 2004). However, relatively little is known about the causes of these patterns and how these habitat features affect small-scale (<1 m) patchiness of species (Hogue and Miller 1981; Barros et al. 2004; Gallucci et al. 2005). Several studies in physically active, sandy sediments suggest that active selection by post-larval stages is responsible for distribution patterns associated with microtopographic features (e.g., Sameoto 1969; Grant 1981). If active selection occurs, then patterns may be a result of faunal responses to a variety of different food patches produced by small-scale variations in water flow (VanBlaricom 1982; Snelgrove and Butman 1994; Barros et al. 2004).

Previous quantitative macrofaunal sampling in sandy rippled beds at the Long Term Ecosystem Observatory (LEO-15) on the continental shelf off New Jersey revealed



strong differences in species-specific patterns of abundance in crests and troughs (e.g., Newby 2006; see Chapter 2). Specifically, the deposit-feeding polychaete, *Polygordius jouinae*, is commonly found in higher and more variable densities in ripple troughs compared to crests (see Chapter 2). Patches of fine organic flocs have also been observed by divers on the surface of ripple troughs in sandy sediments at LEO-15 (Petrecca, pers. comm.). Patchiness of resources coupled with the behavior of species can determine the arrangement of individuals within communities (Thrush et al. 1989) and it was the observations described above that laid the foundation for the present study. This study first set out to reconfirm distribution patterns observed for *P. jouinae* in rippled beds at LEO-15 (see Chapter 2) and to determine ambient concentrations of food resources at the same spatial scale. Then, using a laboratory flume, and a flat sandy bed, we also tested whether these patterns could be causally related to active selection by *P. jouinae* for elevated levels of sedimentary particulate organic matter derived from the organic-rich flocs typically associated with troughs. We predicted that (1) *P. jouinae* will detect and choose a more favorable habitat (i.e., areas with relatively higher amounts of sedimentary particulate organic matter), (2) the movement of *P. jouinae* will be directed (i.e. in response to some stimulus associated with the sedimentary organic matter) rather than in an undirected search pattern until sedimentary organic matter is located (i.e. no stimulus detected), (3) sediment choice will depend on the location of sedimentary organic matter in relation to a worm's starting position (downstream or upstream of the food source).

## MATERIALS AND METHODS

### Study site and species

The Long-term Ecosystem Observatory (LEO-15), (39° 27.69' N, 74° 15.81' W) is located on the inner continental shelf off New Jersey, USA. Sediments in this area include well-sorted, medium to coarse sands with a median grain size of 400-500  $\mu\text{m}$  (Reimers et al. 2004). Sediments are subjected to both unidirectional currents and wave-driven, oscillatory flow. During a particularly active period from August-September 1995, mean alongshore currents (measured 44 cm above the bottom) were 5 to 20  $\text{cm s}^{-1}$  and cross-shore currents associated with the tides were generally  $\leq 8 \text{ cm s}^{-1}$  (Traykovski et al. 1999). Rippled beds are the predominant bedform with ripple heights ranging from 3 to 15 cm and wavelengths of 10 to 100 cm (Traykovski et al. 1999; Styles and Glenn 2002). During the present study 2006, ripples were 6 to 12 cm in height and had a wavelength of 14 to 30 cm.

The study species was the small (sexually mature adult body length 13.0-43.1 mm; width 0.23-0.38 mm) interstitial, deposit-feeding polychaete *Polygordius jouinae* which is a dominant member of infaunal communities in sandy sediments at LEO-15, and in bays and harbors from Massachusetts to southern New Jersey (Ramey et al. 2006). This species has a certain fidelity to coarse sandy sediments, and density has been shown to be significantly positively correlated with the proportion of medium to very coarse sand and negatively correlated with fine sand at relatively large scales (Ramey et al. 2006). However, considerable variation and patchiness occurs at small spatial scales (Grassle et al. 1999).

### Sample collection

The observation that *P. jouinae* is commonly found in higher but more variable densities in ripple troughs compared to crests came from samples collected at LEO-15 on several dates in 1994 and 1995 (see Chapter 2). Paired sediment cores (7-cm diameter, 10 cm deep, 38.5 cm<sup>2</sup>) from ripple crests and troughs (90 cores total), were randomly collected by SCUBA divers from Stations 9 and 30 (see map Weissberger and Grassle 2003; see Chapter 2) and processed over a 300- $\mu$ m sieve. In May 2006, to determine if these patterns for *P. jouinae* were still present, and to determine sediment parameters, which were not included in the 1994 and 1995 studies, the same methods were used to haphazardly collect paired crest-trough samples at Station 9 ( $n=12$ ) and Node B ( $n=6$ ) (see map Ma and Grassle 2004). To aid in setting up the experiments described below, a small amount of sediment was removed from the top layer ( $\sim 1$  cm deep) of each core, prior to fixation, and frozen for later determination of ambient concentrations of total chlorophyll-*a* and phaeophytin, as an indirect measure of food availability. Samples were then washed over stacked 300- $\mu$ m and 32- $\mu$ m sieves and fixed separately. Following removal of *P. jouinae* from the sediment retained on the 300- $\mu$ m sieve, grain size analysis was conducted for Node B samples (re-combined 300- $\mu$ m and 32- $\mu$ m portions) using dry weights and stacked sieves ( $\geq 2$  mm, 1 mm, 500  $\mu$ m, 250  $\mu$ m, 125  $\mu$ m, 32  $\mu$ m,  $\leq 32$   $\mu$ m). Sediment to be used in the experiments and live *P. jouinae* were collected from troughs at Node B. Sediment was either frozen directly or briefly washed over a 100- $\mu$ m mesh to remove some of the particulate organic matter and then frozen, thus creating sediments with relatively high and low amounts of organic matter (+ or – organic matter respectively). To ensure consistency among experiments, total organic carbon,

chlorophyll-*a*, and phaeophytin were determined for these sediments each time an experiment was run. Sediment for carbon and nitrogen analysis was first dried, ground, and acidified in silver cups to remove carbonates and then measured using a Fisons NA1500N elemental analyzer with acetanilide as a calibration standard. Sample chl *a* and phaeophytin was extracted from sediment (3-11 g) in 90% acetone and determined by fluorometric analysis using the low sensitivity setting on the Hitachi F2000 spectrofluorometer (modified from Strickland and Parsons 1972; APHA 1992).

#### Flume and experimental setup

All experiments were conducted in the racetrack flume at the Institute of Marine and Coastal Sciences, Rutgers University, New Jersey (<http://marine.rutgers.edu/flume/racetrk.html>) designed after the flume described by Nowell et al. (1989) (Fig. 6.1). Experiments were conducted in the straight working section (6.2 m long, 0.7 m wide). For each experiment, two plates (30 cm × 30 cm) were placed in the flume 1.5 m apart (plate 1 upstream of plate 2), and separated by a cross-channel bedload trap in the flume bottom (described by Stocks 2002) (Fig. 6.1). The bedload trap opening was flush with the flume bed 21.5 cm downstream of plate 1. This was designed to catch any worms moving as bedload, thus preventing worms from plate 1 being transported into plate 2. For each experiment the flume was filled with natural seawater to a depth of 14 cm, maintained at 20 °C, with a salinity of 31 ±2. Flow is driven by a set of paddles located in the return channel of the flume and free stream velocity was set at 5 cm s<sup>-1</sup> which is comparable to the mean flow at LEO-15 (Traykovski et al. 1999; Styles and Glenn 2002). Due to the large number of worms needed for the experiments, it

was necessary to reuse worms. Individuals, however, were never used in consecutive experiments and were carefully monitored throughout the study to make sure they remained healthy (i.e. were active, undamaged, and had few intestinal parasites). *P. jouinae* used in the experiments were adults 21 to 30 mm in length. Worms were maintained at ~20 °C in small bowls with seawater and + organic matter sediment which was regularly renewed. Prior to all experiments, worms were starved for ~24 h.

#### Experiment 1: distribution patterns

This experiment was designed to examine distribution patterns and determine if *P. jouinae* shows a preference for sediment type given a choice between sediments with relatively high and low amounts of organic matter under flow conditions (constant grain size), or moves predominantly in the upstream or downstream direction regardless of sediment type. It is also possible that movement is a result of some combination of these factors (i.e. sediment type and flow direction). Each plate, described above, was made up of two arrays (each 10 cm × 10 cm; 1 cm deep) arranged side by side (6 cm apart) (Fig. 6.2). Arrays were further subdivided into four equal sized cells with a temporary plastic divider. Three of the arrays were designated as treatment arrays (3 replicates) and one as a control. Cells in the treatment arrays were filled with sediment containing either relatively high (+ organic) or low amounts of organic matter (– organic) in an alternating pattern (Fig. 6.2). For the control, all cells contained – organic matter. With the plastic divider present, five worms were placed in the center of each cell ( $5 \text{ worms cell}^{-1} = 20 \text{ worms array}^{-1} \times 4 \text{ arrays} = 80 \text{ worms trial}^{-1}$ ) and given 30 min to burrow into the sediment. The plastic divider was then removed, flow started, and after 48 h the number

of worms in each cell was counted. This experiment was performed four times (referred to as trials 1-4;  $n=320$  worms) and each time the location of the control array was changed so it had occupied all four possible positions after completion of the four trials. To determine if shear velocity ( $u_*$ ) was similar among arrays within and among experimental trials, flow velocities were measured in the center of  $\geq 2$  cells array<sup>-1</sup> during most experiments (for exceptions, see Table 6.2). Measurements were taken at 7-12 heights above the sediment bed with a 2-axis (measuring horizontal and vertical components of velocity) Laser Doppler Velocimeter (LDV). Graphical presentations of the vertical flow profiles indicated that two points (8 and 12 cm above the bed) were above the log layer and they were not used in the calculation of  $u_*$  (cm s<sup>-1</sup>) (Nowell et al. 1981).

#### Experiment 2: direction of movement

This experiment was designed to determine if the patterns observed for *P. jouinae* in the first experiment were a result of *P. jouinae* moving in a directed search (i.e. in response to some stimulus associated with the sedimentary organic matter) or not (i.e. did not detect a stimulus and moved in some non-directed search pattern), and if success locating an organic patch depends on the location of the patch in relation to the worm's starting positions (downstream or upstream of the food resource). Here, the two plates were each divided into 12 elongate cells (24 cm × 1 cm; 1 cm deep) spaced 1.5 cm apart (Fig. 6.3). Each cell was filled with – organic matter sediment with the exception of a small patch (2 cm × 1 cm) containing + organic matter. This patch was randomly placed (by flipping a coin) so for 50% of the cells it was located 3 cm upstream of the worm,

(worm placed at the center of each elongate cell, at the 12-cm mark), and in the remaining 50% of the cells it was 3 cm downstream of the worm (Fig. 6.3). To accomplish this, the patch was placed at a 3 cm distance from the center of each elongate cell (i.e. at distances of 7-9 cm or 15-17 cm along the 24-cm long cell). Three cm was chosen because it is comparable to the total length of the worms. A straw ~2 cm long was inserted into the sediment in the center of each cell (at 12-cm), and a single worm was placed in each straw. Straws were flush with the bottom of the plate to prevent premature movement of the worms. Once the worms had burrowed into the sediment, the straws were removed, and the flow was started. Thus, worms were given a 50:50 chance of locating a patch or not, or to find a patch by moving with the flow (downstream) or against it (upstream). After 30 min the flow was stopped and a plastic divider was inserted where the worm had initially been placed. Sediment was then removed in 1-cm increments (from the side without an organic patch first) to determine if the worm had moved in the direction of the + organic patch and the distance it had moved from its starting position ( $1 \text{ worm cell}^{-1} \times 12 \text{ cells} \times 2 \text{ plates} = 24 \text{ worms trial}^{-1}$ ). This experiment was performed three times (herein referred to as trials 1-3;  $n=72$  worms). Since free stream velocity was the same as in experiment 1 and because values were similar among arrays and trials, flow profiles were not conducted.

### Data analysis

Patterns of abundance for *P. jouinae* in rippled beds were compared by plotting mean ( $\pm$ SD) density for paired crest-trough samples. Experiment 1 was designed to test the prediction that the distribution of *P. jouinae* is dependent on the amount of organic

matter in the sediment and/or flow direction (upstream/downstream). Thus, if sediment type was important then significantly more worms were expected in the + organic sediment cells, whereas, if flow direction was most important significantly more worms would be present in the two upstream cells or the two downstream cells in each array.

Other patterns could result if both sediment type and flow direction were important (this interaction was tested using a Chi square goodness of fit test ( $\chi^2$ ), described below).

Experiment 2 was designed to test the prediction that movement of *P. jouinae* is associated with a chemical stimulus from sedimentary organic matter and success in locating an organic patch will be greater if the patch is located upstream of the worm's starting position. Therefore, significantly more *P. jouinae* were expected to move toward patches located upstream of their starting position (movement against the flow).

Distribution patterns (Experiment 1) and direction of movement (Experiment 2) were analyzed using a Chi square goodness of fit test ( $\chi^2$ ) which was calculated for each experimental trial (Experiment 1: number of worms pooled for replicate treatment arrays  $n=60$ , control  $n=20$ ; Experiment 2:  $n=24$ ), ( $\alpha=0.01$  and  $0.05$ ). Since results and environmental parameters (i.e. sediment type, flow direction [upstream vs downstream] and interaction between sediment type and flow) were consistent among experimental trials, a Chi square test was also performed on pooled trial data (Experiment 1: number of worms pooled for treatment arrays for trials 1-4,  $n=240$ , control  $n=80$ ; Experiment 2 trials 1-3:  $n=72$ ). Experimental results are presented graphically for sediment type since it was the only variable that significantly affected the distribution of *P. jouinae*.



## RESULTS

### Density of *P. jouinae* and ambient sediment parameters

The density of *P. jouinae* was greater in ripple troughs compared to crests at Station 9 and 30 in several months during 1994 and 1995 (Fig. 6.4). Density was also generally more variable in replicate trough samples than in replicate crest samples. Despite the low density of *P. jouinae* in May 2006 these patterns were still present. Mean density of *P. jouinae* in ripple troughs at Sta. 9 was 3.5 ( $\pm 2.42$ ) ind.  $38.5 \text{ cm}^{-2}$  compared to 0.33 ( $\pm 0.82$ ) ind.  $38.5 \text{ cm}^{-2}$  in crests, whereas, at Node B, mean density in troughs was 7.33 ( $\pm 5.03$ ) ind.  $38.5 \text{ cm}^{-2}$  and 0.33 ( $\pm 0.58$ ) ind.  $38.5 \text{ cm}^{-2}$  in crests. In the same May 2006 samples, concentrations of chl *a* and phaeophytin within the top centimeter of sediment were generally low and more variable in troughs (Sta. 9:  $0.18 \times 10^{-3}$  -  $0.48 \times 10^{-3} \text{ mg g}^{-1}$ ; Node B:  $0.19 \times 10^{-3}$  -  $3.0 \times 10^{-3} \text{ mg g}^{-1}$ ) than in crests (Sta. 9:  $0.20 \times 10^{-3}$  -  $0.30 \times 10^{-3} \text{ mg g}^{-1}$ ; Node B:  $0.40 \times 10^{-3}$  -  $5.0 \times 10^{-3} \text{ mg g}^{-1}$ ). Chl *a* and phaeophytin concentrations were  $\sim 1.33$  times greater in ripple troughs ( $\bar{x} = 0.33 \times 10^{-3} \text{ mg g}^{-1}$ ) than crests ( $\bar{x} = 0.25 \times 10^{-3} \text{ mg g}^{-1}$ ) at Sta. 9 and  $\sim 4.88$  times greater in troughs ( $\bar{x} = 2.4 \times 10^{-3} \text{ mg g}^{-1}$ ) than crests ( $\bar{x} = 0.49 \times 10^{-3} \text{ mg g}^{-1}$ ) at Node B (Table 6.1). Sediment grain size was similar among crests and troughs at Node B (Table 6.1). The coarse to medium sand fraction, and fine sand fraction made up  $\sim 93.9\%$  and  $\sim 5.3\%$  respectively in crests, and  $\sim 91.2\%$  and  $\sim 7.6\%$  in troughs (Table 6.1).

### Sediment and flow parameters for experiments

Sediment used in the experiments was similar in grain size to that in rippled beds at LEO-15 and did not differ among experimental treatments (i.e., + organic matter vs - organic matter) (Table 6.1). The range of total chl *a* and phaeophytin concentrations used for the + organic ( $0.32 \times 10^{-3}$  -  $0.60 \times 10^{-3}$  mg g<sup>-1</sup>) and the - organic treatments ( $0.12 \times 10^{-3}$  -  $0.21 \times 10^{-3}$  mg g<sup>-1</sup>) were similar to the range observed among crests and troughs, and within troughs at Sta. 9 (Table 6.1). Chl *a* and phaeophytin concentrations were ~3.27 times greater in the + organic treatment than the - organic treatment, and similar to the elevated values at Node B. Total sediment organic carbon values were low and were ~1.7 times higher in the + organic treatment ( $\bar{x}=0.035\%$ ) compared to the - organic treatment ( $\bar{x}=0.021\%$ ) (Table 6.1). C/N ratios were similarly low which suggests that organic matter present was relatively fresh. Shear velocity ( $u_* = 0.32 \pm 0.11$  cm s<sup>-1</sup>) in Experiment 1 was similar among arrays within experiments and among experimental trials (Table 6.2).

### Experiment 1: distribution patterns

In each of the four trials >90 % of the *P. jouinae* were found in the + organic matter cells after 48 h (Fig. 6.5). A Chi square goodness of fit ( $\chi^2$ ) test on pooled data for each trial indicated that the distribution of *P. jouinae* was dependent on sediment type ( $\alpha=0.01$ ) and independent of flow direction (Table 6.3). In a single trial (trial 2) distribution was also dependent ( $\alpha=0.05$ ) on the interaction between sediment type and flow direction. A Chi square test on pooled data from trials 1-4 produced the same results for sediment type and flow direction, however, there was no significant interaction

between these two variables (Table 6.3). At the end of 48 h fecal pellets produced by the worms were concentrated on the surface of cells with the + organic matter (Fig. 6.6). In the four control arrays *P. jouinae* remained relatively evenly distributed among the four cells in each trial and worm distribution was independent of flow (Table 6.3).

#### Experiment 2: direction of movement

In each of the three experimental trials 43% to 45% of worms were found in the + organic patch after 30 min (6.7). Similar numbers of worms were present in patches located upstream (percentage of worms=60%, 50%, 50% trials 1-3, respectively) and downstream (percentage of worms= 40%, 50%, 50% trials 1-3, respectively) of the worm's starting position. A Chi square goodness of fit ( $\chi^2$ ) test on pooled data for each trial indicated that direction of movement by *P. jouinae* was independent of sediment treatment (+ organic patches) and flow (upstream vs downstream) (Table 6.4). In 30 min worms showed a wide range in movement, ranging from 1 cm to 11 cm ( $2.93 \pm 2.02$ ;  $n=42$ ) from their starting position, however, it is important to note that it is unknown what path worms took during this experiment and if they were found at the end of the 12-cm cell, whether they had traveled >12 cm during the experiment. Average rate of movement was  $0.1 \text{ cm min}^{-1}$  and the highest rate was  $0.4 \text{ cm min}^{-1}$ .

## DISCUSSION

This study was motivated by unpublished observations in 1994 and 1995 that showed certain infaunal species have distribution patterns associated with either crests or

troughs in rippled beds at the LEO-15 research site off New Jersey (see Chapter 2). Specifically, the deposit-feeding polychaete, *Polygordius jouinae*, occurred in higher but more variable densities in ripple troughs compared to crests in inner continental shelf, sandy sediments. This pattern was confirmed with samples taken for the present study in 2006. We hypothesized that this small-scale distribution pattern might be established by an interaction between the behavior of the worm and the effects of unidirectional near, bottom flows on the distribution and concentration of particulate organic matter within the sediments.

Replicated flume experiments showed that contrary to our initial expectations, worms did not detect patches of organic-rich sediment at a distance as little as 3 cm, even when patches lay upstream of the worm. Yet, in the absence of a directed search, worms were clearly capable of moving rapidly through the interstices of these coarse sandy sediments under realistic flow conditions (free stream velocity of  $5 \text{ cm s}^{-1}$ ;  $u_* = 0.32 \text{ cm s}^{-1}$ ). Once worms found an organic-rich patch of sediment they remained in it and fed long enough to produce small mounds of fecal pellets on the sediment surface. Thus, *P. jouinae* was capable of habitat choice, even though discovery of patchy sediment resources appears to be a chance process.

Spatial and temporal variations in the distribution and concentration of particulate organic matter is likely a key determinant in influencing benthic infaunal distribution patterns in high energy, physically active, shallow coastal and continental shelf benthic environments characterized by a rich array of microtopographic features, and well sorted sandy sediments with low concentrations of sediment organic matter. The significant role microtopography plays in advective transport of water through the interstices of the

sediment has been identified as a key process enhancing the deposition, transport, and patchiness of organic matter in permeable shelf sands (Huettel et al. 1996; Pilditch et al. 1998; Reimers et al. 2004). In sandy rippled beds, near bottom water containing particulate organic matter and oxygen, is pumped into the sediments in ripple troughs, where organic matter may become trapped, whereas pore water is pumped out at the apex of crests (Huettel et al. 1996; Ziebis et al. 1996; Huettel and Webster 2001). Particulate organic matter may also accumulate in troughs by settling there as a result of reduced shear stress. In the present study, we found concentrations of chl *a* and phaeophytin up to five times higher in ripple troughs compared to crests. Similar patterns in total chl *a* and phaeophytin concentrations have been found for paired crest-trough samples collected at LEO-15 (39° 27.0' N, 74° 4.27' W) in October 2005 with higher ( $\sim 6.6$  times) and more variable concentrations in troughs ( $3.6 \times 10^{-3} \pm 3.2 \times 10^{-3} \text{ mg g}^{-1}$ ) relative to crests ( $0.55 \times 10^{-3} \pm 0.10 \times 10^{-3} \text{ mg g}^{-1}$ ) (Taghon, pers. comm. unpubl.). Although percentage of particulate organic carbon was not compared among ambient crests and troughs at LEO-15 in the present study, sediment treatments contained levels similar to those determined for samples haphazardly collected at Node B, LEO-15 by Rusch et al. (2003) (0.015 % to 0.030 %) depending on sediment depth and season. Such low levels are typical of sandy sediments. In the North Sea, particulate organic carbon levels in sediments with coarse (i.e.  $672 \pm 78 \text{ } \mu\text{m}$ ) and medium ( $299 \pm 8 \text{ } \mu\text{m}$ ) grain sizes and a variety of microtopographical features such as mounds, pits, and ripples were 0.030 % and 0.023 % respectively (Janssen et al. 2005).

These surrogate measures of food concentrations and densities of *P. jouinae* were patchily distributed in sediments at similar spatial scales at LEO-15 and in spite of low

overall concentrations of total chl *a* and phaeophytin and particulate organic carbon, our experiments indicate that a difference of ~3.0 and 1.5 times respectively between sediment patches (values consistent with ambient concentrations), appears to affect the behavior of *P. jouinae* deposit-feeder. In general, active selection by infauna for food resources has often been implicated, rather than experimentally tested, in explaining observed patterns associated with rippled beds. For example, predatory amphipods have been observed to occur in higher abundances beneath ripple crests along with their meiofaunal prey, whereas ripple troughs contained higher abundances of sand-browsing amphipods (Fenwick 1984). Small-scale spatial patterns of nematodes, not directly associated with either crests or troughs in an intertidal rippled bed in Yaquina Bay Oregon, were believed to result from nematodes actively responding to regularly distributed food aggregations consisting of particulate organic matter and its associated bacteria which had been buried by migrating ripples (Hogue and Miller 1981). Although higher densities of *P. jouinae* in ripple troughs was a spatially and temporally consistent pattern at LEO-15, patterns in rippled beds are not always consistent. Newby (2006) found higher abundances of surfclams, *Spisula solidissima*, in either crests or troughs at LEO-15 depending on location and date, but this bivalve species is a suspension feeder not a deposit feeder.

For organisms living in such a dynamic, heterogeneous, and patchy environment with oscillatory flow a strategy of undirected movement such as exhibited by *P. jouinae*, rather than a response to a chemical stimulus from a distance seems advantageous. This, in combination with high mobility, likely allows *P. jouinae* to respond relatively quickly to changing conditions such as exhaustion of a local food resource. Even though

movement was undirected, it is likely that different patterns of behavior in sediments containing higher versus lower amounts of particulate organic matter allow this worm to aggregate, at least for a time, in more favorable organic-rich sediments. The capability of *P. jouinae* to remain in a favorable sediment patch was further examined by placing a single worm in the center of one of the – organic cells using the same array as in Experiment 1 and recording the appearance of new fecal pellets, at ~3-h intervals for 7 d (Ramey and Bodnar, unpubl.). The first fecal pellet(s) were found after 21 and 33 h and these, along with the worm and successive pellets, were present in/on the surface of one of the + organic patches for the entire week. The polychaete, *Protodrilus hypoleucus*, was shown to glide along with little variation in speed of movement in unfavorable sands (i.e. sterile sands), whereas, upon entering more favorable sands with associated bacteria, it moved much more slowly and intermittently stopped to sample the sediment within its reach by moving its head in various directions (Gray 1967). It is likely that *P. jouinae* employs a similar pattern of behavior.

Relatively little is known about this interstitial environment or how organisms react to it (Vogel 1981). Interstitially, viscous forces predominate (low Reynolds numbers ~0.2) and meiofaunal organisms (size classes i.e. 0.01 cm – 0.10 cm), typically experience flows of about one body length per second and shear stresses of ~0.003 to 0.05 N m<sup>-2</sup> (Crenshaw 1980; Vogel 1981). Crenshaw (1980) found that meiofauna have higher mobility at high flows and that movement in sandy sediments is predominantly in the upstream or downstream direction rather than across the flow. In our system, where the patch of + organic sediment filled the elongate channels in Experiment 2, a worm that moved toward a patch regardless of whether it was upstream or downstream of the

worm's starting position would be bound to encounter it after moving 3 cm (i.e. approximately one body length). Life in sandy sediments has been described as living in an array of parallel channels (Crenshaw 1980; Vogel 1981). Rates of movement up to  $0.4 \text{ cm min}^{-1}$  for *P. jouinae* means that a worm could potentially travel the wavelength of a typical ripple (14-30 cm) at LEO-15 in 35-75 min. Members of the Family Polygordiidae are often considered part of the meiofaunal community because they spend their post-settlement life interstitially, however, their length (1.0 cm to 10.0 cm) also makes them part of the macrofaunal community as it is usually defined. Perhaps the relatively large size of *P. jouinae* (sexually mature adult body length 1.3 to 4.3 cm) may allow it to move with relative ease through coarse but not finer sandy sediments.

Very few selection experiments involving subsurface movement of post-larval polychaetes have been conducted since those of Gray in the mid-1960's (e.g., Gray 1967; Gray 1974) where *Protodrilus rubropharyngeus* and *P. hypoleucus* were shown to actively select for particular grain-sizes and organic surface films on sand grains produced by certain species of bacteria. Although microorganisms were not identified or quantified in the present study it is unlikely that the microbial composition of the sediment was changed significantly by washing it over a 100- $\mu\text{m}$  sieve to create the – organic treatment, and thus sediment choice is believed to be based on the amount and quality of the organic matter and associated bacteria. Several meiofaunal organisms have also been shown to migrate to and select food patches of some species of algae but not others (Lee et al. 1997), although movement patterns were not examined. Moreover, in an experiment more similar to the present research, Nilsson et al. (2000) tested whether the oligochaete *Paranais litoralis*, could choose patches of sediment based on sediment



quality at small spatial scales (patch diameter 2.5 cm) over 48 h in still water. Worms selected more favorable sediment patches containing sediment from the field which was renewed every 3 d, over nutrient-exhausted sediment (sediment from the field that was not renewed over 30 d). However, depletion of resources also triggered a swimming response. Worms emerged from the sediments into the water column, and selected sediment which was not resource depleted upon resettling.

There is some evidence that recently settled juvenile *P. jouinae* (length categories 6 and 9 mm) may be transported to ripple troughs from surrounding sediments via re-suspension or bed load transport in the field. In a reciprocal sediment transplant experiment at LEO-15, hydrodynamically unbiased trays placed in ripple troughs contained recently settled juvenile *P. jouinae* within 3 to 5-d (Snelgrove et al. 1999). Tray design precluded movement through the sediment by these worms. Juvenile worms concentrated in the upper sediment layer may be more easily resuspended than adults living deeper in the sediment. A preliminary experiment in the racetrack flume (modeled after Stocks 2002), showed that significant numbers of adult *P. jouinae* did not actively emerge from unfavorable inorganic sediments at a free stream velocity of  $18 \text{ cm s}^{-1}$  (Ramey and Ballew, unpubl.). The present study could not determine the relative importance of active and/or passive re-suspension versus subsurface migration in creating and maintaining the higher density of this deposit feeder in ripple troughs compared to crests. It does show that the affinity of adult *P. jouinae* for higher levels of organic matter and its undirected, high rate of subsurface movement is a plausible mechanism for creating and maintaining observed patchiness of this species in continental shelf sediments.

## CONCLUSIONS

Paired ripple crest-trough samples taken from stations located kilometers apart, in several months in 1994, 1995, and in May 2006 consistently found higher but more variable densities of *P. jouinae* in troughs compared to crests. Sedimentary organic matter was also patchily distributed at similar spatial scales. In a racetrack flume under realistic flow ( $u_* = 0.32 \text{ cm s}^{-1}$ ) and flat bed conditions, arrays of alternating fresh ambient sediment (+ organic) and freshly sieved sediment (-organic) showed significant subsurface movement of *P. jouinae* to sediment patches containing higher amounts of particulate organic matter (+ organic) in 48 h. Subsequent experiments showed that locating + organic patches was not the consequence of a directed search since *P. jouinae* did not detect favorable patches with higher amounts of organics at a 3-cm distance, even when patches were located upstream of the worm. However, worms that located + organic patches remained there and fed. Rate of movement in sediments indicated that *P. jouinae* could potentially travel the wavelength of a typical ripple (14-30 cm) at LEO-15 in 35-75 min. Thus in a dynamic environment where food concentrations are low and patchy, the affinity of *P. jouinae* for particulate organic matter and its undirected, high rate of subsurface movement, is a plausible mechanism to account for the similar spatial distributions of *P. jouinae* and its food resources in continental shelf sediments.

Table 6.1: Means ( $\pm$ SD) for sediment parameters including v-coarse to med= very coarse to medium sand (%), fines (%), chl *a* and phaeophytin= total chlorophyll *a* and phaeophytin ( $\text{mg g}^{-1}$ ), particulate organic carbon (%), nitrogen (%), and C:N ratio for + organic and – organic experimental sediment treatments and for ambient LEO-15 sediments from crests and troughs. N/A=not available.

Sediment parameters	Experiments		LEO-15 ambient	
	+ organic	- organic	crest	trough
v-coarse to med (%) (250 $\mu\text{m}$ - 1 mm)	89.5 ( $\pm 0.5$ )	92.0 ( $\pm 2.2$ )	Node B 93.9 ( $\pm 2.0$ )	Node B 91.2 ( $\pm 1.2$ )
fines (%) (63-125 $\mu\text{m}$ )	10.2 ( $\pm 0.16$ )	8.3 ( $\pm 2.2$ )	Node B 5.3 ( $\pm 2.1$ )	Node B 7.6 ( $\pm 0.6$ )
chl <i>a</i> and phaeophytin ( $\text{mg g}^{-1}$ )	$0.49 \times 10^{-3}$ ( $\pm 0.12 \times 10^{-3}$ )	$0.15 \times 10^{-3}$ ( $\pm 0.04 \times 10^{-3}$ )	Sta. 9 $0.25 \times 10^{-3}$ ( $\pm 0.04 \times 10^{-3}$ ) Node B $0.49 \times 10^{-3}$ ( $\pm 0.10 \times 10^{-3}$ )	Sta. 9 $0.33 \times 10^{-3}$ ( $\pm 0.10 \times 10^{-3}$ ) Node B $2.4 \times 10^{-3}$ ( $\pm 0.56 \times 10^{-3}$ )
organic carbon (%)	0.035 ( $\pm 0.002$ )	0.021 ( $\pm 0.004$ )	N/A	N/A
nitrogen (%)	0.004 ( $\pm 0.001$ )	0.002 ( $\pm 0.001$ )	N/A	N/A
C:N	8.1 ( $\pm 1.22$ )	8.9 ( $\pm 0.41$ )	N/A	N/A

Table 6.2: Shear velocity ( $u_*$ ) ( $\pm$ SD) for  $\geq 2$  cells array<sup>-1</sup> (with a few exceptions,  $n=1$ ) on the upstream and downstream plate positions in the racetrack flume, for a single array across all 4 experimental trials and for all 4 arrays in a single trial measured with a laser doppler velocimeter during Experiment 1.

Location	Experiment 1: shear velocity cm s <sup>-1</sup> ( $u_*$ )				
	Trial 1	Trial 2	Trial 3	Trial 4	Trial 1-4
upstream array 1	0.27 $\pm$ 0.05 $n=2$	0.25 $\pm$ 0.03 $n=2$	0.32 $\pm$ 0.10 $n=3$	0.42 $\pm$ 0.20 $n=3$	0.33 $\pm$ 0.13 $n=10$
upstream array 2	0.24 $\pm$ 0.02 $n=3$	0.24 $\pm$ 0.03 $n=2$	0.44 $\pm$ 0.10 $n=3$	0.40 $\pm$ 0.15 $n=3$	0.34 $\pm$ 0.13 $n=11$
downstream array 3	0.37 $\pm$ 0.14 $n=4$	0.27 $\pm$ 0.01 $n=3$	0.38 $\pm$ 0.13 $n=3$	0.25 $n=1$	0.33 $\pm$ 0.11 $n=11$
downstream array 4	0.30 $n=1$	0.26 $\pm$ 0.06 $n=4$	0.29 $\pm$ 0.02 $n=2$	0.28 $n=1$	0.27 $\pm$ 0.04 $n=8$
Total	0.30 $\pm$ 0.09 $n=10$	0.26 $\pm$ 0.03 $n=11$	0.37 $\pm$ 0.10 $n=11$	0.38 $\pm$ 0.13 $n=8$	0.32 $\pm$ 0.11 $n=40$

Table 6.3: Chi square goodness of fit ( $\chi^2$ ) values for four environmental parameters including sediment type (+ organic vs – organic; df=1), flow (up=upstream and down=downstream; df=1), interaction between sediment type and flow (df=1) and total (df=3) calculated for treatment arrays ( $n=3$ ) and control arrays ( $n=1$ ) in 4 trials ( $(\chi_{\text{trial1}})^2$ ,  $(\chi_{\text{trial2}})^2$ ,  $(\chi_{\text{trial3}})^2$ ,  $(\chi_{\text{trial4}})^2$ ) conducted in experiment 1 (i.e. number of worms were pooled for replicate treatment arrays  $n= 60$ , control  $n= 20$ ). Since results were consistent among trials ( $n=4$ ), a Chi square test was also performed on pooled trial data ( $[\chi_{\text{tot(1-4)}}]^2 = \chi^2$  for trials 1-4,  $n= 240$ , control  $n=80$ ). \* =  $\alpha=0.01$  and \*\* =  $\alpha 0.05$ .

<b>Experiment 1: distribution patterns</b>						
<b>Treatment</b>						
Source	df	$(\chi_{\text{trial1}})^2$	$(\chi_{\text{trial2}})^2$	$(\chi_{\text{trial3}})^2$	$(\chi_{\text{trial4}})^2$	$(\chi_{\text{tot(1-4)}})^2$
Sediment type	1	*40.02	*40.02	*36.82	*43.35	*165.00
Flow (up or down)	1	0.15	0.42	0.42	0.017	0.038
Interaction	1	1.83	**4.23	3.43	1.70	1.76
Total	3	*42.00	*44.67	*40.67	*45.07	*166.80
<b>Control</b>						
Source	df	$(\chi_{\text{exp1}})^2$	$(\chi_{\text{exp2}})^2$	$(\chi_{\text{exp3}})^2$	$(\chi_{\text{exp4}})^2$	$(\chi_{\text{tot(1-3)}})^2$
Flow (up or down)	1	0.05	0.45	1.25	0.05	1.01
Total	3	0.40	2.80	4.40	1.20	4.90

Table 6.4: Chi square goodness of fit ( $\chi^2$ ) values for environmental parameters including sediment type (+ organic vs – organic; df=1), flow (up=upstream and down=downstream; df=1), interaction between sediment type and flow (df=1), and total (df=3) calculated for each trial 1-3 ( $(\chi_{\text{trial1}})^2$ ,  $(\chi_{\text{trial2}})^2$ ,  $(\chi_{\text{trial3}})^2$ ) conducted in experiment 2 (i.e. worms pooled for replicate treatment arrays  $n=24$ ). Since results were consistent among trials ( $n=3$ ), a Chi square test was also performed on pooled trial data ( $(\chi_{\text{tot(1-3)}})^2$  = trials 1-3,  $n=72$ ). \* =  $\alpha=0.01$  and \*\* =  $\alpha=0.05$ .

<b>Experiment 2: direction of movement</b>					
Source	df	$(\chi_{\text{trial1}})^2$	$(\chi_{\text{trial2}})^2$	$(\chi_{\text{trial3}})^2$	$(\chi_{\text{tot(1-3)}})^2$
Sediment type	1	0.17	0.17	0.42	1.18
Flow (up or down)	1	0.17	0	0.08	0.01
Interaction	1	0.49	0.31	0.50	0.37
Total	3	0.83	0.48	1.00	1.54

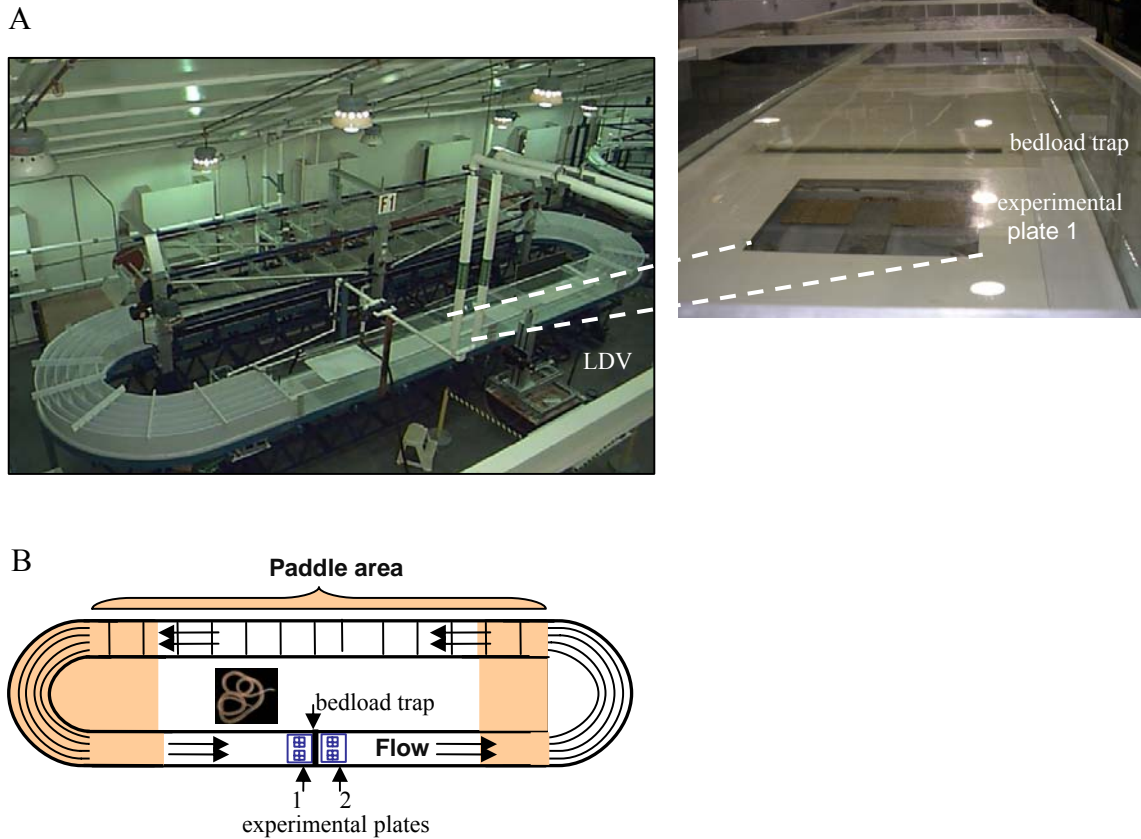


Fig. 6.1. A. Digital image and B. diagram (from above) of the racetrack flume at the Institute of Marine and Coastal Sciences, Rutgers University, New Jersey. Experiments were conducted in the straight working section (front straight section) of the flume which contained two experimental plates (plate 1 upstream of plate 2), separated by a cross-channel bedload trap. Flow was driven by a set of chain-drive paddles (back straight section) and stream velocity was set at  $5 \text{ cm s}^{-1}$ . Arrows in (B) indicate flow direction and the Laser Doppler Velocimeter (LDV) is visible in front of the working section of (A).

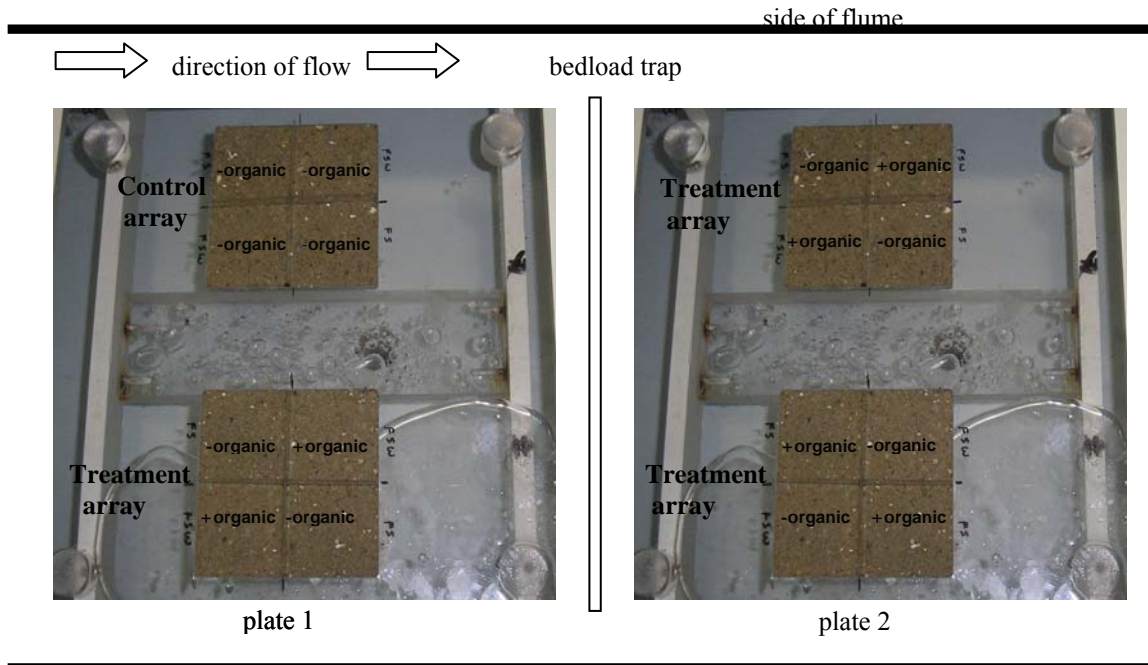


Fig. 6.2. Experiment 1 (distribution patterns): experimental plates containing one control array and three treatment arrays (each 10 cm × 10 cm; 1 cm deep) each subdivided into four equal sized cells with a temporary plastic divider. Treatment array cells were filled with sediment containing either relatively high (+ organic) or low amounts of organic matter (– organic) in an alternating pattern. The control array was made up of – organic matter. Five worms were placed in the center of each cell ( $5 \text{ worms cell}^{-1} = 20 \text{ worms array}^{-1} \times 4 \text{ arrays} = 80 \text{ worms trial}^{-1}$ ).



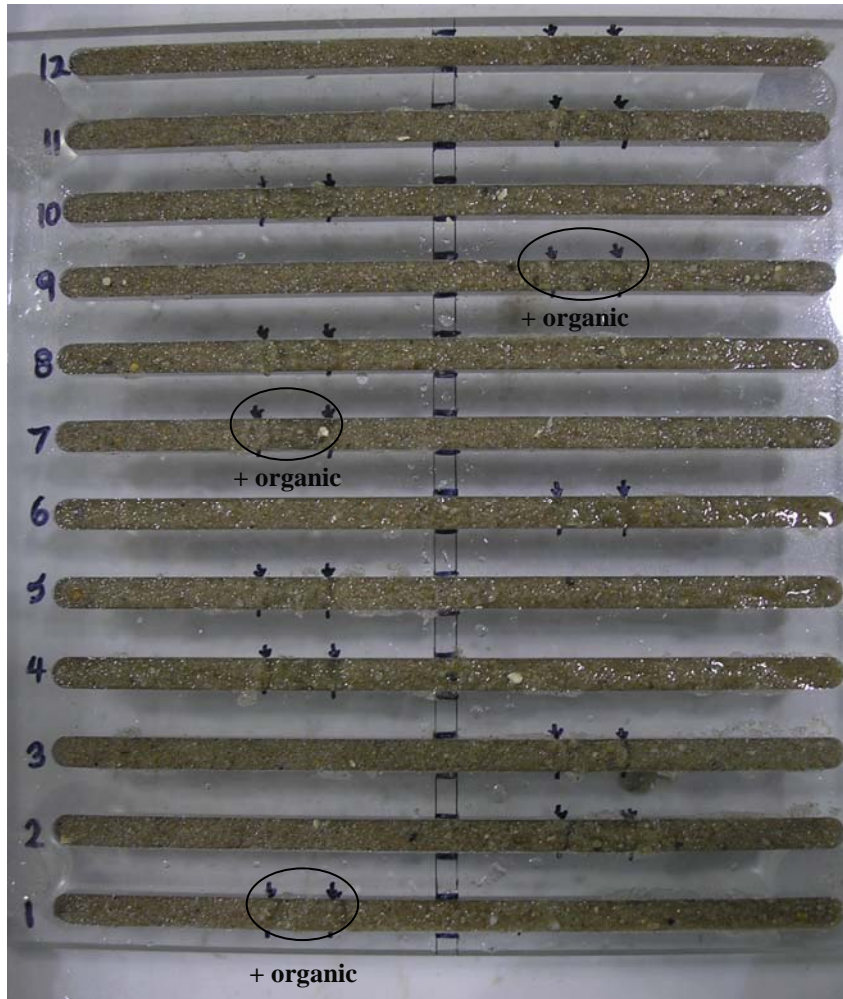


Fig. 6.3. Experiment 2 (direction of movements): experimental plate divided into 12 elongate cells ( $24\text{ cm} \times 1\text{ cm}$ ;  $1\text{ cm}$  deep) spaced  $1.5\text{ cm}$  apart. Each cell was filled with – organic matter sediment with the exception of a patch ( $2\text{ cm} \times 1\text{ cm}$ ) containing + organic matter. This patch was randomly placed so for 50% of the cells it was located  $3\text{ cm}$  upstream of the worm, (worm placed at the center of each elongate cell, at the  $12\text{-cm}$  mark), and in the remaining 50% of the cells it was  $3\text{ cm}$  downstream of the worm.

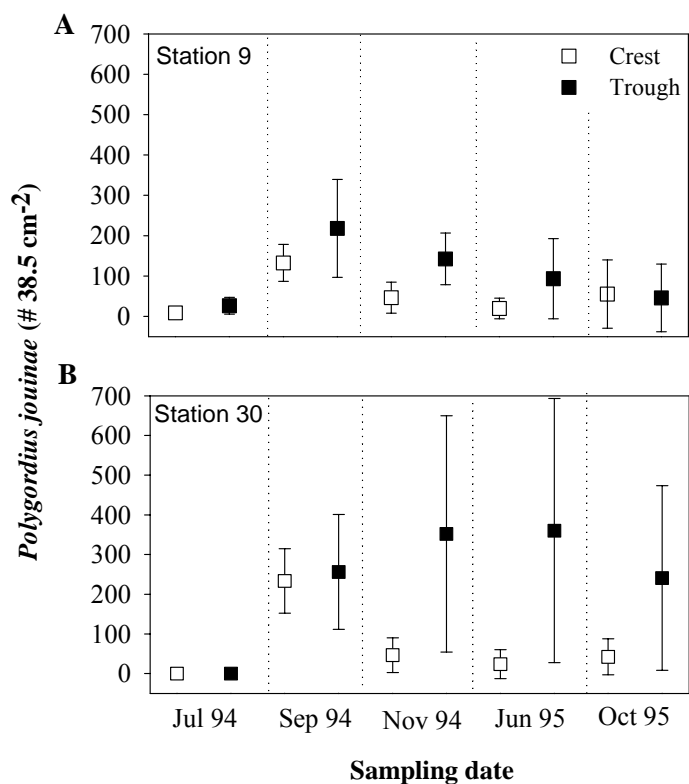


Fig. 6.4. Mean ( $\pm$ SD) density of *Polygordius jouinae* (number 38.5 cm<sup>-2</sup>;  $n=9$ ) in paired crest and trough samples collected from (A) station 9 and (B) station 30 at LEO-15 research site located on the inner continental shelf off New Jersey, during July, September, November 1994, and June and October 1995 (Grassle et al., unpubl.).

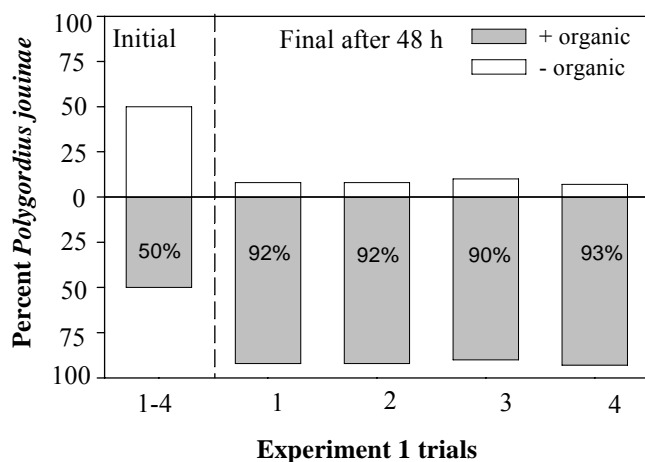


Fig. 6.5. Percentage of *P. jouinae* present in + organic matter and – organic matter sediment treatments at the beginning of the experiment (initial conditions) and after 48 h, under flow conditions (free stream velocity  $5 \text{ cm s}^{-1}$ ; shear velocity  $u_* = 0.32 \pm 0.11 \text{ cm s}^{-1}$ ) in racetrack flume for four trials in experiment 1 ( $n = 80 \text{ trial}^{-1}$ ;  $n = 320$ ).

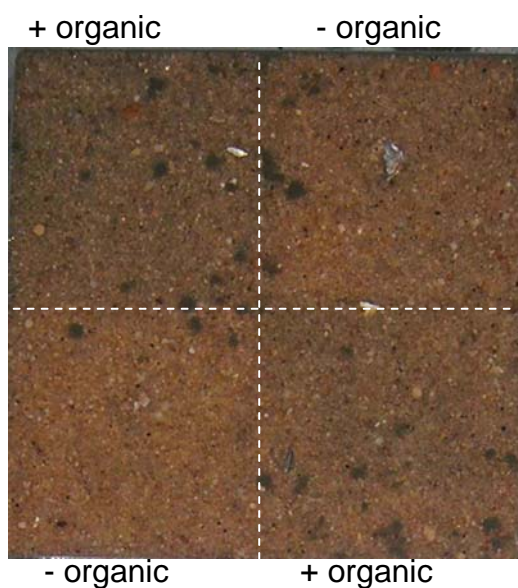


Fig. 6.6. Distribution and aggregation of fecal pellets on sediment surface of + organic sediment patches of a representative treatment array (each 10 cm  $\times$  10 cm; 1 cm deep) after 48 h, experiment 1. Array is subdivided into four equal sized cells (shown with dashed lines) containing + organic and –organic sediments.

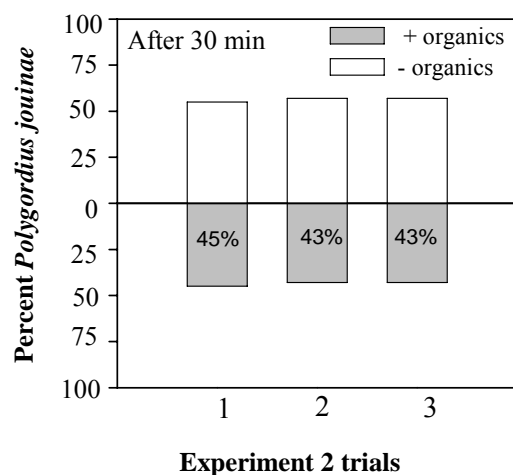


Fig. 6.7. Percentage of *P. jouinae* present in + organic matter patch and – organic matter sediment after 30 min under flow conditions (free stream velocity  $5 \text{ cm s}^{-1}$ ) in racetrack flume for three trials in experiment 2, irrespective of positions upstream or downstream of the worm's starting position ( $n=24 \text{ trial}^{-1}$ ;  $n=72$ ).

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## CURRICULUM VITA

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### Education

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1998-2001	M.Sc. in Biological Sciences (with distinction) Memorial University of Newfoundland, Canada
2001-2008	Ph.D. in Ecology and Evolution Rutgers, The State University of New Jersey, New Brunswick, NJ

### Employment

1994-1995	Field and Laboratory Environmental Research Technician Kejimikujik National Park and Acadia Center for Estuarine Research, Nova Scotia, Canada
1994-1997	Biology Laboratory demonstrator Acadia University, Nova Scotia, Canada
1998-2000	Biology Laboratory demonstrator Memorial University, Newfoundland, Canada
2000-2001	Oceanographic Assistant Fisheries Conservation Chair, Fisheries and Marine Institute, Newfoundland, Canada
2001-2002	Teaching Assistantship Rutgers University, New Jersey, USA
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### Publications

**Ramey, P.A.** and Bodnar, E. Selection by a deposit-feeding polychaete, *Polygordius jouinae*, for sediment enriched with organic flocs (Limnology and Oceanography, in revision)

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